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The Snail Polygyra thyroidus as a Mycophagist

FRED T. WOLF AND FREDERICK A. WOLF

(WITH ONE FIGURE)

It has been known for many years that fungi represent an important source of food for molluscs. On the basis of their food requirements, Stahl (1888) divided the slugs into two categories: "omnivora," which show no marked preferences in their choice of food, and "specialists," which feed almost entirely upon fungi. The slugs *Limax maximus*, *L. cereus*, and *Arion subfuscus* were found by Stahl to be mycophagous. Voglino (1895) has observed that the spores of a number of agarics, including *Tricholoma humile*, *Mycena alcalina*, *Lactarius deliciosus*, *Russula* sp., and *Inocybe fastigata*, after passage through the digestive tract of slugs, are still capable of germination.

The extensive researches of Gain (1891), Buller (1909, 1922), Benecke (1918), and Elliott (1922) on the feeding habits of certain of the species of *Limax*, *Agrolimax*, *Amalia*, and *Arion* have indicated that approximately a hundred species of such fleshy basidiomycetous fungi as *Armillaria*, *Boletus*, *Collybia*, *Coprinus*, *Cortinarius*, *Hypholoma*, *Laccaria*, *Lactarius*, *Lepiota*, *Paxillus*, *Psalliota*, *Russula*, and *Tricholoma* are readily eaten by slugs. These animals also consume with avidity other basidiomycetes as *Polyporus squamosus*, *P. sulphureus*, and *Lycoperdon caelatum*, and a number of ascomycetous fungi including *Peziza vesiculosa*, *P. aurantiaca*, *P. badia*, *Bulgaria polymorpha*, and *Morchella esculenta*. It is of interest to note that slugs are apparently capable of eating without the slightest ill effects the fruiting bodies of *Amanita caesarea*, *A. mappa*, *A. muscaria*, *A. pantherina*, *A. phalloides*, *A. porphyrea*, *A. pustulata*, *A. rubescens*, *A spissa*, *A. strobiliformis*, and *A. umbrina*, all of which are poisonous to man (Stahl, 1888; Voglino, 1895: Benecke, 1918; Buller, 1909, 1922).

Apparently very little is known concerning the feeding of snails upon fungi. Gain (1891) has found that a number of fleshy basidiomycetes are readily eaten by the snails *Zonites nitidulus*, *Helix arbustorum*, *H. aspersa*, *H. cantiana*, *H. hispida*, *H. hortensis*, *H. nemoralis*, *H. rotundata*, *H. sericea*,

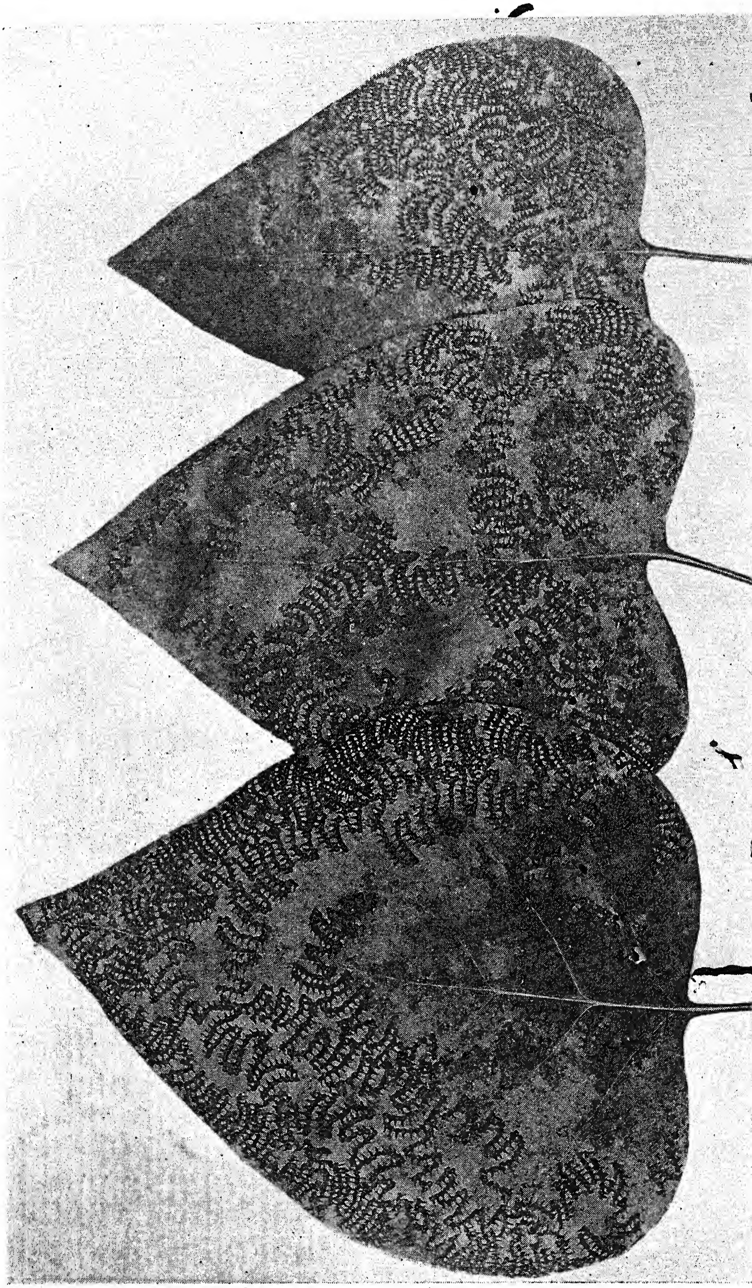

Fig. 1. Leaves of lilac infected with *Microsphaera alni*, showing the feeding track made by *Polygyra thryoidus* (about two thirds natural size).

and *H. virgata*. Certain observations by Ludwig (1891) are of especial interest in connection with the present paper, since he noted that a number of plant parasitic fungi are eaten by snails. These included the downy mildew *Peronospora gangliformis* on *Cirsium oleraceum*, two powdery mildews, *Sphaerotheca castagnei* on hops (*Humulus lupulus*), and *Erysiphe horidula* on *Symphytum officinale*, and several species of rust fungi. The powdery mildew fungus on hops was eaten by *Helix fruticum*, while the *Erysiphe* was consumed by *Succinea putris*.

In the summer of 1938, the foliage of lilac, *Syringa vulgaris*, in certain yards in Durham, N. C. was infected by the powdery mildew *Microsphaera alni* (DC.) Wint. to the extent that most of the leaves were rather uniformly covered with the characteristic profuse whitish powdery coating. On a few leaves however, there occurred peculiar serpentine markings as though the coating had been etched. The appearance of such leaves, shown in Fig. 1, strongly suggested the possibility that some small animal had eaten away the fungus coating and had thus made the markings. To test this assumption examinations were made at night with the result that snails were noted to be present upon leaves bearing designs that appeared to have been freshly made. Furthermore when some of these snails were transferred to leaves uniformly covered with mildew and observations were then made after a brief period, it was convincingly apparent that the intricate patterns were produced by these animals while feeding. The snails were identified as *Polygyra thyroidus* Say by Mr. G. W. Wharton* of the Department of Zoology. This species is described by Pratt (1935) and was illustrated, under the name *Helix thyroides* Say, in the monograph by Tryon (1887).

Patterns of identical design have been observed to occur abundantly on several species of unidentified crustose lichens occurring on trees within the Duke Forest and on the upper surface of the sporophores of *Polyporus picipes* Fr.

The designs made by *Polygyra thyroidus* are very similar in appearance to those of *Helix aspera* as illustrated by Taylor (1894). The formation of these designs is the result of the following procedures as determined by direct observation of the process: the snail extends its body from the shell and, while moving the anterior part in a clockwise direction, removes the fungus coating, using successive strokes of the radula. A narrow arc-shaped band, devoid of fungus, is thereby produced. Then the snail moves forward approximately an eighth of an inch and clears a similar

* Thanks are extended Mr. G. W. Wharton for this identification and for the specimens of *Polyporus picipes*.

arc, moving the anterior part of its body in a counter-clockwise direction. Although the snail moves in a more or less straight line the serpentine feeding track becomes the resultant of the two synchronized activities, feeding and moving forward. The symmetrically disposed spines on one margin of the track are produced by the radular teeth, the apices of the spines being in the direction of advance of the snail.

In order to determine whether fungi other than *Microsphaera alni* were eaten by *P. thyroidus*, a number of snails were secured and placed in small glass jars into which various fungi were introduced. It was found that *Uncinula australiana* McAlpine on *Lagerstroemia indica*, *Erysiphe cichoracearum* DC. on *Zinnia elegans*, and *Erysiphe polygoni* DC. on *Trifolium pratense* were readily eaten by *P. thyroidus*. Patterns similar to those on lilac were produced in each case. Fruiting bodies of the slime mold, *Fuligo septica* Gmelin, the ascomycete, *Hypomyces lactifluorum* (Schw.) Tul. parasitic on *Russula* sp., and the basidiomycetes, *Cantharellus aurantiacus* Fr., *Boletus* sp., *Lactarius piperatus* (L.) Pers., *Russula emetica* Fr., *Russula virescens* Fr., and *Amanita verna* Bull. were also eaten by these snails. They also consumed the lichen, *Sticta herbacea* (Huds.) Ach.

Although the number of organisms tested was rather small, it is perhaps worthy of note that not a single one of the species tested was refused by Polygyra. Furthermore, in cases in which the snails were permitted to choose between two or more fungi simultaneously present in the jars, a marked preference for *Microsphaera alni* was shown. All of the fungi tested were eaten by *P. thyroidus* in preference to lettuce or other chlorophyll-containing food. It is evident, therefore, that *P. thyroidus* should be considered as mycophagous according to the classifications of Stahl (1888) and Benecke (1918).

There are a number of problems of general biological and theoretical interest about which inferences may be drawn on the basis of these observations. One of these is concerned with the possible spread of powdery mildew by means of snails. Inasmuch as the actual distance travelled by a snail within a given time interval is so short, and since an examination of the contents of the digestive tract and of the fecal pellets of *P. thyroidus* failed to give definite evidence that mildew spores pass through intact, it does not seem probable that snails are of appreciable importance in the dissemination of powdery mildews.

Another problem, of interest to zoologists, is concerned with the means by which a land snail locates the powdery mildew on leaves several feet above the ground. The experiments of Buller (1922) with the slug, *Limax maximus*, have clearly demonstrated the perception by this animal

of chemotropic stimuli exerted by such fungi as *Phallus impudicus*, *Boletus scaber*, *Cortinarius caninus*, *Russula heterophylla*, and *R. nigricans*. The odors of these fungi were found to be perceived by *L. maximus* at distances ranging from 10 to 21 feet. Whether or not the attraction of snails to fungi is to be explained solely on the basis of chemotropism can be settled only after further experimentation.

SUMMARY

The snail *Polygyra thyroidus* Say was observed under natural conditions to eat the powdery mildew *Microsphaera alni* on lilac, in consequence of which a feeding track of peculiar and characteristic design is produced on lilac leaves. Similar tracks were found on crustose lichens and on the sporophores of *Polyporus picipes*. Under laboratory conditions, *P. thyroidus* was found to eat *Uncinula australiana* on *Lagerstroemia indica*, *Erysiphe cichoracearum* on *Zinnia elegans*, *E. polygoni* on *Trifolium pratense*, making similar markings. It also consumed *Fuligo septica*, *Hypomyces lactifluorum* on *Russula* sp., *Stictis herbacea*, *Cantharellus aurantiacus* *Boletus* sp., *Lactarius piperatus*, *Russula emetica*, *R. virescens*, and *Amanita verna*. *P. thyroidus* is decidedly mycophagous in regard to its food preferences.

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Studies in the Ericales IV. Notes on Chimaphila, Gaultheria and Pernettya in Mexico and Adjacent Regions

W. H. Camp

An accumulation of material received for identification as well as specimens collected during my own field studies in the state of Oaxaca, Mexico, during the winter of 1936–1937, make it advisable at the present time to publish brief notes on a miscellany of certain American ericaceous genera and species. All specimens cited, unless otherwise noted, are in the Britton Herbarium at the New York Botanical Garden.

CHIMAPHILA

Chimaphila maculata (L.) Pursh, Fl. Am. Sept. 300. 1814.

Chimaphila maculata acuminata Lange, Vidensk. Meddel. **1867:** 112. 1868.

Chimaphila acuminata (Lange) Rydb. N. Am. Flora **29:** 31. 1914.

Chimaphila guatemalensis Rydb. N. Am. Flora **29:** 32. 1914.

Chimaphila dasystemma Torr.; Rydb. N. Am. Flora **29:** 32. 1914.

The entering wedge on the break-up of this species in Mexico and Central America was begun by Lange with *C. maculata acuminata* and continued by Rydberg (N. Am. Flora **29:** part 1. 1914) with the elevation of this variety to specific rank and the addition of *C. guatemalensis* and *C. dasystemma* as new. Being familiar with *C. maculata* as it occurs throughout its range in the United States and having seen it on various occasions in Mexico, as well as having the types of *C. dasystemma* and *C. guatemalensis* available, in addition to a considerable series of the several species involved, I am unable to see a greater degree of variation within the bulk of the Mexican and Central American material of this group than that within the material from the United States. It is to be admitted that there exists a tendency for some of the Mexican specimens to be somewhat more narrow-leaved and, on this basis, it might be easy to maintain them as *C. maculata acuminata* Lange, were it not for the fact that, in this region, others of the specimens are wider-leaved and less acuminate than some scattered throughout the range of the species in the United States. Too, it must be remembered that in Mexico this species grows at much greater altitudes than in the United States. This would tend somewhat to modify the leaf form since in Mexico it grows mainly between the elevation of 5000 and 8000 feet.

The type of *C. dasystemma* is a small, oval-leaved specimen, obviously abnormal and not matched in any other Mexican material, but is matched by homologous, abnormal forms from the United States. The type of *C.*

guatemalensis, characterized by long tubules on its anthers, is merely a robust specimen, matched, or even exceeded, in this character by our own material from various stations in the eastern United States. It is therefore thought best to return these entities to the basic species and consider them merely as biotypic parts of a more widespread, ancient and not particularly variable species, *Chimaphila maculata* Pursh.

CHIMAPHILA MENZIESII (R. Br.) Spreng.

During the above study, several specimens placed under *C. dasystemma* by Rydberg were seen which did not seem to be conspecific with *C. maculata* (*sensu lata*). Examination indicated that they were unusually robust individuals of *C. Menziesii*. A further study of this species revealed a rather continuous variation of robustness and degree of maculation from its northern limits southward through Washington, Oregon, and California, culminating in the very robust and considerably maculated forms in Mexico. Having personally studied this species as it occurs in the field in the Pacific Northwest, I admit that the Mexican material is quite different from it, but the Californian material intergrades to such an extent that no sharp line of demarcation may be drawn between the forms. Here again, I am, as yet, not inclined to recognize any taxonomic entities where such intergrades, seemingly the result of differences in water supply, insolation, and altitude, are to be found.

The specimens which increase the range of *Chimaphila menziesii* are as follows: MEXICO. Sonora: Pineridge Pass, *Hartman* 351, Dec. 17, 1890 (in fruit). Jalisco: Sierra du Narayit (Territoire Huichol), *Leon Diquet*, without number of date (in bud).

The extension of range of *C. menziesii* into Mexico is not surprising, but the inclusion of certain other described species under *C. maculata* will no doubt, meet with some disapproval. In this connection, however, it must be recorded that field study, at least in Oaxaca, of various species of Mexican plants segregated by earlier writers, leads me to conclude that there is a much closer affinity between certain members of this flora and that of the United States than has previously been supposed. Also, the complexity of the Oaxacan flora in many groups would seem to indicate that this part of southern Mexico, with its great ranges of mostly non-volcanic mountains, is one of the critical regions in a study of the dispersal of the floras of Central America, the Caribbean flora, the derived floras of north-central Mexico and the ancient Tertiary flora of the southern Appalachians. Except for brief mention, further discussion of this topic is outside the scope of the present paper.

GAULTHERIA

In preparation for a more complete review of the Ericaceae (*sensu lata*), Dr. Sleumer, of Berlin, from time to time has published miscellaneous papers relating to the genera and species of this group. In the identification of certain specimens of the genus *Gaultheria* it was necessary to consult and, if possible, follow his work. I have not always been able to do this because it is my opinion that Sleumer, at times, has misinterpreted certain American species, possibly because he has never had the privilege of seeing them growing in the field. A discussion of selected species follows.

In a recent revision of the species of *Gaultheria* of Mexico and Guatemala (Notizbl. **12**: 285–287. 1935), Sleumer, in his key, divides that group of species which generally are without glandular pubescence on the inflorescence on the basis of the shape of the calyx-lobes, following the lead of both Small (N. Am. Flora **29**: 74. 1914) and Standley (Contrib. U. S. Natl. Herb. **23**: 1092. 1924). In this way *G. acuminata* Cham. & Schlecht. is separated by its supposedly deltoid, acute calyx-lobes from the other members of the group with elongate-deltoid, acuminate calyx-lobes. It is my opinion that the retention of this as a key character is most unfortunate since it seems clear after examination of a considerable number of specimens and study of these plants as they occur in the field, that it is a distinction without a difference.

Actually, to return to the genus as a whole, so far as I can determine, there are two rather well defined groups in the Mexican species of *Gaultheria*: (1) The ACUMINATAE, in which the rachis is either glabrous or finely puberulent (or rarly with minute glands), and (2) The ODORATAE, in which the rachis is hirsute and in all but a few species with the hairs gland-tipped.

THE ACUMINATAE

In most treatments, *G. acuminata* Cham. & Schlecht. is listed as having a distribution limited to the state of Vera Cruz. Actually, it is more widespread, to my present knowledge ranging from Vera Cruz and Oaxaca to central Mexico. The supposedly restricted range of this species is due, probably, to confusion with *G. nitida* Benth.

This last (*G. nitida*), has been placed in synonymy under *G. ovata* DC. by Sleumer. Not having seen the type of *G. ovata*, I am unable either to confirm or disagree with this decision. However, if the two are synonymous, I can not agree with the position in the key as assigned by Sleumer, for the corollas of the type collection of *G. nitida* are somewhat densely puberulent and not glabrous as he has indicated. To be sure, the pubescence is not prominent, but the fact that it is ferruginous causes it to blend

so well with the color of the corollas on this century-old specimen that it might easily be missed.

Since I have not studied types of either *G. ovata* DC, or *G. laevigata* Mart. & Gal., I am unable at present to dispose of them in conjunction with *G. nitida* Benth. and *G. Nelsonii* Small, all more or less closely related to the earlier *G. acuminata*. *G. nitida*, if one may judge from the type, differs from *G. acuminata* at least in the absence of punctations on the lower surface of its leaves, a character shared (*ex descr.*) by *G. laevigata* Mart. & Gal. These "punctations," in reality the bases of either glandular or non-glandular, deciduous hairs, have rarely been noted as having taxonomic significance. I am not certain how much weight should be placed on such a character but specimens at hand would seem to indicate that *G. nitida* is a separate entity, closely related to, but distinct from *G. acuminata*. I therefore propose the following:

GAULTHERIA ACUMINATA Schlecht. & Cham. var. **nitida** (Benth.) Camp, stat. nov.

Gaultheria nitida Benth. Pl. Hartw. 45. 1840.

MEXICO. Hidalgo: "in loco 'Banco' dicto," *Hartweg* 344, 1840 (type of *G. nitida* Benth.). Puebla: Honey Station, 5600 ft. *Pringle 8961*. Oaxaca: High pass between Tamazulapa and Ayutla (near Zempoaltepetl), *Camp 2724, 2726*.

A further problem is the disposition of *G. Nelsonii* Small. This species is characterized by having its inflorescence and corolla completely glabrous. While possible that such characteristics may be a further variation of *G. acuminata*, it is, nevertheless, strongly suspected that *G. Nelsonii*, with its completely glabrous inflorescence and corollas and somewhat oblong leaves is distinct from the complex of forms surrounding *G. acuminata*. Until the type of *C. laevigata* is seen, the writer is unable to ascertain whether Sleumer is correct in placing this species in synonymy under *G. laevigata* Mart. & Gal.

In the group of specimens related to the ACUMINATAE on the basis of the nature of the pubescence of the inflorescence, the following unusual ones were noted, being sufficiently different to warrant the description of the following two new species.

Gaultheria Pringlei Camp, sp. nov.

Frutex 1–2.5 m., ramis glabris; folia ovato-oblonga, petiolo 5–9 mm. longo, basi rotundata vel late cuneata, apice abrupte acuminata, subcoriacea, 6–10 cm. longa, 2.5–5 cm. lata, supra obscure punctata, subtus in foliis adultis punctata, sed in foliis junioribus dense ferrugineo-glandulosa, margine obscure

serrulata; racemi laterales et subterminales 12–20-flori, 7–8 cm. longi; rachis albido-puberula, supra medium glandulosa, pedicelli graciles albido-puberuli 4–8 mm. longi, bractea glabra; calyx campanulatus, lobis 5 deltoideis acuminatis puberulis margine subciliatis 1.5 mm. longis; corolla urceolata apice manifeste contracta circ. 5.5 mm. longa, sparse glanduloso-hirsuta; stamina 10, filamentis basi dilatatis sparse vel dense pilosulis circ. 2 mm. longis, antheris circ. 2 mm. longis; ovarium depresso-globosum, dense ferrugineo-pilosum, stylo glabro.

Gaultheria Pringlei is a coarse shrub to 2.5 meters, its leaves ovate-oblong with petioles 5–9 mm. long, basally rounded to broadly cuneate, apically abruptly acuminate, subcoriaceous, 6–10 cm. long and 2.5–5 cm. wide, their upper surfaces obscurely punctate with deciduous gland-hairs, the lower surface of the adult leaves punctate, in the younger densely set with minute gland-hairs, the margin obscurely serrulate; the racemes lateral and subterminal 7–8 cm. long, bearing 12–20 flowers; the rachis densely white-puberulent, bearing scattered gland-hairs about 0.25 mm. long on its upper portion, or in specimens other than the type, extending even to the base; pedicels slender, white-puberulent, 4–8 mm. long, the basal bracts glabrous, somewhat variable, but generally broad and only about half as long as the pedicels or rarely as long; calyx campanulate, its 5 lobes deltoid-acuminate, puberulent and subciliate on the margin, the lobes about 1.5 mm. long at anthesis; corolla urceolate and apically contracted, about 5.5 mm. long, sparsely glandular-hirsute; stamens 10, filaments basally dilated, sparsely to densely pilose, about 2 mm. long, anthers about 2 mm. long; ovary depressed-globose, densely ferrugino-pilose, style glabrous.

MEXICO. Vera Cruz: Sand Bluffs near Jalapa, 4000 feet, *C. G. Pringle 8336*, May 15, 1900 (type, N. Y.); Acultzinco, *E. Matuda 1159*(*B*).

At first glance, if judged only by the foregoing description, it would seem that *G. Pringlei*, on the basis of the gland-hairs found on the rachis, might perhaps be placed in the ODORATAE rather than the ACUMINATAE. This glandular pubescence, however, is of a type totally different from that investing many of the members of the ODORATAE. Neither is it to be thought that this species is intermediate between these species groups and it is altogether possible that *G. Pringlei* and the next may yet be considered as sections different from either of the others now recognized.

In connection with this discussion, it might be noted that the type specimen cited above (*Pringle 8336*) in a measure was responsible for a slight misinterpretation of *G. acuminata* by the late Dr. J. K. Small. In his description of this last species (N. Am. Flora **29**: 76. 1914) he states that the

staminal filaments are glabrous. His dissections of this specimen (which he placed in *G. acuminata*) were mounted in glycerin-jelly, a medium which occasionally obscures certain types of pubescence. A reexamination of new dissections as well as the original by means of special lighting, reveals a reasonably abundant pubescence on this structure.

Gaultheria chiapensis Camp, sp. nov.

Frutex, ramis glabris; folia ovata vel lanceolata, petiolo 3–7 mm. longa, basi rotundata, apice sub-acuminata, sub-coriacea, 4–10 cm. longa, 1.5–3.5 cm. lata, supra glabra, subtus dense punctata, margine serrulata; racemi laterales et subterminales 20–30-flori, 6–10 cm. longi; rachis albido-puberula; pedicelli graciles albido-puberuli 5–9 mm. longi, bractea glabra 6–8 mm. longa; calyx campanulatus, lobis 5 acutis puberulis, circ. 2 mm. longis margine subciliatis; corolla urceolata apice manifeste contracta circ. 5 mm. longa, puberula et sparse hirsuta, eglandulosa; stamina 10, filamentis basi dilatatis pilosulis circ. 2 mm. longis, antheris circ. 2 mm. longis; ovarium globosum, dense albido-pilosum, stylo glabro.

Gaultheria chiapensis is apparently a coarse shrub, with glabrous branches, leaves narrowly ovate or sometimes lanceolate as on the type, petioles 3–7 mm. long, basally rounded, apically acute or subacuminate to a calloused tip, subcoriaceous, 4–10 cm. long, 1.5–3.5 cm. wide, glabrous above and densely puncate below, the margin serrate; racemes lateral and subterminal, 20–30 flowered, or in others than the type fewer flowered, 6–10 cm. long; rachis white-puberulent; pedicels slender, white-puberulent, 5–9 mm. long, bracts glabrous, 6–8 mm. long; calyx campanulate, lobes 5, acute, puberulent, about 2 mm. long, their margins subciliate; corolla pink(?), urceolate, apically manifestly contracted, about 5 mm. long, puberulent and sparsely hirsute, the hairs eglandular; stamens 10, filaments basally dilated, pilose, about 2 mm. long, anthers about 2 mm. long; ovary globose, densely white-pilose, style glabrous.

MEXICO. Chiapas: "Cero de Mapastepec," *E. Matuda 2041*, January, 1938 (type, N. Y.); Mt. Pasitar(?), *Matuda 1009;* "Cero de laguna," Mapastepec, 2100 meters, *Matuda 2041-A* (Herb. Univ. Mich.).

This last collection (*Matuda 2041-A*), first issued under the collector's number *2041*, but changed before being called to my attention, is mainly in fruit and while perfectly conspecific with the type—the remaining corollas matching exactly—is interesting in that it shows what probably is an extreme condition of the species. This specimen consists of a portion of a flowering branch about 30 cm. long and bearing not less than 20 racemes, most of which approach the size given as the upper limit of those on the type. The leaves are much more broadly oval than those of the type

and where fully developed, are 5–7 cm. long and 4–4.5 cm. wide. The plant is therefore a coarse shrub probably not less than 1 m. high and may even exceed 2 meters.

THE ODORATAE

GAULTHERIA ODORATA Willd.

Typical of the Mexican and Central American species of this group is *G. odorata*, the type of which came from Venezuela. It seems to be fairly common in the mountains of northern South America and ranges from there northward through Central America into Mexico. With the specimens immediately available, it would appear that *G. odorata*, typically a coarse shrub, with abundant, glandular hairs on the rachis, pedicels, calyx, and corolla, is fairly common in Guatemala but known to me from Mexico only by the following: *Seler 2097*, from Chiapas; and *Conzatti 4110*, from the District of Teotitlán, Oaxaca. In his revision, Sleumer (loc. cit.), has united *G. hidalgensis* Loes. with this species. Not having seen the type of this last, I am unable to check certain characters important in the correct understanding of this group, but I am inclined to agree with him in his conclusions.

GAULTHERIA LANCIFOLIA Small.

The glandular pubescence of the calyx lobes (or rather, the nearly complete lack of it) plays an important role in the interpretation of this species, which was also placed in synonymy under *G. odorata* by Sleumer. It is obvious that the two are closely related and that *G. lancifolia* is a derivative at the northern edge of the range of *G. odorata*, but is easily separable from the basic species on the nature of its calyx. Typically, the calyx of *G. lancifolia* is completely glabrous, except for a line of cilia along the margin of its lobes. The sudden break at the line of the receptacle from the densely puberulent pedicels, thickly set with coarse gland-hairs, to the glabrous calyx-base is striking and a feature not seen in typical material of *G. odorata*. To be sure, there is some variation for occasional calyces (as a small percentage on the type specimen) bear a few short scattered gland-hairs, but these are always near the *apex of the calyx lobes*, in contradistinction with *G. hidalgensis* where (*ex descr.*) they are *more abundant* and confined to the *base of the calyx*, and with *G. odorata* where there is a *complete and abundant* vesture of these hairs on the calyx.

Specimens examined and typical of *G. lancifolia* Small are as follows: MEXICO. Chihuahua: 65 mi. E. of Batopilas, *Goldman 182*. Mexico: Salto de Agua, *Purpus 1774* (type); Nanchititla, *Hinton 7356*. Oaxaca: Zempoaltepetl, middle to upper slopes, *Camp 2662;* ibid., lower slopes,

Camp 2699; high pass between Tamazulapa and Ayutla (near Zempoaltepetl), *Camp 2730*.

Typically, *G. lancifolia* is a rather coarse shrub, sometimes over 1 meter in height, with white or pink corollas. One specimen [*Camp 2662*, Sheet II, collected from the same plant as *Camp 2662*, Sheet I (both in Herb. N. Y. Bot Gard.), but from a stunted, lower branch in shade], while retaining the typical glands on the rachis, has them reduced and rare on the pedicels (the puberulence of the rachis and pedicels as well as the glabrescence of the calyx, is typical), a variation which is to be expected in this species. Also the plants may be lower, as *Camp 2699*, sometimes only half a meter high when growing in dry and exposed habitats. Here the leaves are narrowed, much resembling the type specimen. At higher and, therefore, moister elevations the leaves are broader and closely resemble those of *G. odorata*.

With *G. lancifolia* may be placed this otherwise puzzling form:

GAULTHERIA LANCIFOLIA Small var. **dulcis** Camp, var. nov.

A speciei calyce dense puberulo differt.

Gaultheria lancifolia var. *dulcis* is a coarse shrub 1–2 m. high with leaves closely resembling the species; the gland-hairs on the pedicels are reduced, shorter than typical or even nearly wanting. Its principal point of difference is in having a densely white-puberulent calyx.

GUATEMALA. Dept. Chimaltenango: Santa Eleña, alt. 3000 meters, *Skutch 338*. EL SALVADOR. Volcan de San Salvador, alt. 1000 to 1800 meters, *Paul C. Standley 22944*, April 7, 1922 (type, N. Y.); ibid. *Calderon 477*.

Although somewhat intermediate between typical *G. lancifolia* and *G. odorata* it is thought best to keep this material separate from the species until connecting forms can be found. The puberulence on its calyx is a character often met with in *G. odorata* but the sparsely scattered gland-hairs on its corolla, the almost total lack of them on the calyx, and their reduction in density and size on the pedicels and rachis would seem to place it in closer affinity with *G. lancifolia*. The name is in reference to a note on the type specimen which states that the "fruit" (calyx) is sweet, a character, however, not unusual to this group of species.

GAULTHERIA HARTWEGIANA Loes.

Another species placed in synonymy under *G. odorata* by Small, Standley, and Sleumer is *G. Hartwegiana* Loes. If the original description only were available, it would be easy to reduce this species, but I have examined a photograph of isotype material in the Berlin Herbarium as well as our

own excellently preserved and adequate portion of the type collection (*Hartweg 541*), neither of which agrees in all respects with the original description. It is obvious that a specimen in addition to the type was used to draw up the description (*Seler 2379*, which I have not seen). The largest leaves on the isotypes are rarely over 3 cm. long and never over 2.5 cm. wide, approaching the lower limits set in the original description, which states that they are 2.5–5.5 cm. long and 1.2–3.3 cm. wide. The Berlin specimen, its leaves and stems obviously damaged before collection, is of little help, but our specimen would seem to indicate that the plant was not particularly tall, probably strict, and not spreading, as is typical for *G. odorata*. In our specimen, the leaves, in addition to being smaller, are in proportion shorter and more deeply cordate than is typical for *G. odorata*.

Also interesting in regard to this specimen is its locality of collection. The original description cites it as, "Hab. in Guatemala ad Quezaltenango," whereas the label on our specimen notes it as having been collected "In Mexico, in montibus prope Quezaltenango, Guatemala." Since Mexican territory is only some 60–70 kilometers distant from this locality, it is possible that the temporary headquarters where the specimens were sorted was Quezaltenango but that the collection actually was made in Mexico or at least near the international boundary. This particular region along the border being botanically but little explored, additional material may yet be found which will further authenticate this species.

I maintain that *G. Hartwegiana* Loes. is a valid species, closely related to, but distinct from *G. odorata* Willd. because the leaf-form of *G. Hartwegiana* is obviously different from the general run of the material of *G. odorata* in Mexico and Central America, and because its entire inflorescence is much more densely puberulent than that of *G. odorata* (in which the bracts of the material from Mexico and South America are almost glabrous, except for the marginal cilia and gland-hairs).

GAULTHERIA HIRTIFLORA Benth.

Although a certain amount of confusion is bound to occur between *G. odorata* and *G. hirtiflora*, this last species is quite characteristic, even if a close derivative of *G. odorata*. No single character could be found which would serve absolutely to distinguish the two but *G. hirtiflora* with its nearly deltoid, deeply cordate leaves pubescent with long, persistent gland-hairs on their lower surfaces, is almost unmistakable. Too, the glandular pubescence of this species is much more developed than on *G. odorata*, being more crowded, longer, and with larger glands throughout the entire plant and more persistent on the branches, where they may be as

much as 2 or occasionally 3 mm. long. The largest single plant of *Gaultheria* seen by me in Mexico was one of *G. hirtiflora*. This particular specimen (*Camp 2664*) was growing in the open on the middle slopes of Zempoaltepetl. It was a spreading, gracefully arched shrub 3 meters high and not less than 4 meters in diameter; its leaves deep-green above and glaucous below; at anthesis the rachis, pedicels and calyces were red and the corollas deep-pink to red; at maturity the calyx becomes purplish-black, covering the capsule. The fruit is sweet.

Although *G. hirtiflora* is reported from Guatemala (where it may even be common) I have seen specimens only from the states of Chiapas, Oaxaca, and Puebla in Mexico. Certain Guatemalan specimens with shorter, less dense pubescence and longer leaves would seem to be extremes of *G. odorata*.

Perhaps a further reason for a certain amount of the confusion in regard to *G. odorata*, at least in our American herbaria, was the earlier attempt to include in it the following related but distinct species.

Gaultheria Conzattii Camp, sp. nov.

Frutex ad 0.2 m. altus, ramulis pubescentibus; folia ovalia vel rectangulo-ovata, 2.5–4 cm. longa, 1–2.5 cm. lata, basi subcordata vel rotundata, apice obtusa vel abrupto-acuminata, supra subglabra, subtus pubescentia, pilis sparsis ferruginis, margine minute serrata vel undulata, setosa; racemi terminales, 2–3.5 cm. longi, rachis et pedicelli (circ. 5–9 mm. longi) dense albido-puberuli et ± dense rubro- vel ferrugino-pilosi, minute glandulosi; calyx 5-lobus, lobis acutis vel acuminatis, circ. 2 mm. longis, albido-puberulis, apice sparse glanduloso-hirsutis; corolla urceolata (intense rosea), apice manifeste contracta, strigosa vel crispe pilosa, pilis minute glandulosis vel eglandulosis; stamina 10, circ. 4 mm. longa, filamentis basin versus dilatatis, dense pubescentibus, circ. 2.25 mm. longis, antheris circ. 1.75 mm. longis; ovarium depresso-globosum pubescens.

Gaultheria Conzattii is a low, spreading, subcaespitose shrub to 0.2 m. with villous branches; leaves elliptic to ovate or individually oblong, 2.5–4 cm. long (rarely 5 cm. on sprouts) and 1–2.5 cm. wide, apically obtuse or abruptly acuminate with a fairly prominent calloused tip, basally subcordate to rounded, the margin finely serrate or occasionally undulate, setose, the hairs sometimes lost by mid-winter, the upper surface glabrous except for an extremely minute puberulence along the veins and, in occasional individuals, set with coarse ferruginous hairs mainly on the veins or on a broad band along the margin, the lower surface with abundant coarse ferruginous hairs, persistent on the petioles and larger veins, occasionally deciduous on the blade by mid-winter, petioles about 2 mm. long; inflores-

cence minutely puberulent; racemes 2–3.5 cm. long, rachis villous, the hairs tipped with minute glands or apically clavate, or sometimes individually glandless; pedicels 5–9 mm. long at anthesis, their pubescence of similar character as that of the rachis; bracts linear-oblong to oval, 5–8 mm. long, minutely puberulent to glabrate, their margins ciliate and (except for the lowest) set with the long glandular hairs typical of the inflorescence; bracteoles linear, subulate, or rarely oblanceolate, puberulent and glandular-hirsute; calyx somewhat spreading at anthesis (when dry), its lobes triangular, acute to acuminate, about 2 mm. long, cut about two-thirds of the way to the receptacle, the lobes with ciliate margins, the cilia often tufted at the apex, generally with a few scattered gland-hairs near the apex; corolla deep-pink, about 6 mm. long, urceolate, manifestly contracted at the apex, its lobes ovate, about 0.7 mm. long, strigose or with crisped, often minutely glandular hairs 0.5–1 mm. long, puberulent outside and inside; stamens 10; anthers about 1.75 mm. long; filaments about 2.25 mm. long, basally somewhat enlarged, pubescent on the contracted portion; ovary depressed-globose; style tapering, included; mature fruit not seen.

MEXICO. Oaxaca: Cerro de San Felipe, upper slopes, *W. H. Camp 2416*, Dec. 29. 1936 (type, N. Y.); ibid. *Camp 2870;* ibid. 8–10,000 ft., *Pringle 4679;* ibid. 10,000 ft., *Charles L. Smith 206;* ibid. 3000 meters, *C. Conzatti and V. Gonzáles 407*.

It is a pleasure to dedicate this species to my friend Professor C. Conzatti who, for so many years, has lived in Oaxaca where, every day he has looked up at the top of this mountain and in this, the twilight of his life, recalls days spent on its summit with Pringle and other collectors.

Closely related to *G. Conzattii* and distinct from it only by varietal rank is the following:

GAULTHERIA CONZATTII var. **mijorum** Camp, var. nov.

A speciei rachidibus et pedicellis eglandulosis, calyce subpubescente, margine ciliato differt.

Gaultheria Conzattii var. *mijorum*,[1] like the species with which I have related it, is a subcaespitose shrub, seldom or rarely exceeding 0.2 m. in height and apparently propagating by runners. Like other members of the genus when studied in the field, it proves to be variable, but the crisped, *completely nonglandular hairs* of the inflorescence, at first purplish-

[1] Named for the Mije tribe who inhabit this region and who still carry on their ancient sacrificial rites at an altar just a few meters from the place of collection of the type. For a further account and map see Jour. N. Y. Bot. Gard. **38**: 129–144, 153–170. 1937.

red but later ferruginous, are characteristic. They may be either scattered or dense. The leaves vary from ovate to oval, are 1–4.5 cm. long and fairly coriaceous when completely mature, subglabrous in the type collection, but scattered punctations on the lower surface and along the margin indicate a pubescence much like the species but apparently more completely deciduous, apically generally acute, but occasionally obtuse (particularly on abnormally dwarfed plants), basally rounded, subtruncate, or on the more robust plants subcordate; petioles 1–2 mm. long; racemes terminal or in the upper several nodes, 1–2.5 cm. long; or on extreme plants reduced to a single flower in the axils of the upper several leaves; rachis and pedicels minutely puberulent with white hairs and also bearing loosely set, crisped, nonglandular hairs up to 2 mm. long, the branches similarly clothed for several seasons; bracts glabrous except for the ciliate margin and the marginal gland-hairs (these confined to the upper several bracts); bracteoles much as in the species except that the hairs are apparently eglandular; calyx red, externally glabrous except for a finely ciliate margin, the cilations sometimes tufted at the tips of the lobes, the lobes lanceolate acute, about 2.5 mm. long at anthesis; calyx nearly covering the capsule at maturity, subcarnose and purple-black; corolla pink, urceolate, 6–7 mm. long, pubescent, the hairs on occasional flowers apically enlarged and clavate; capsules finely pubescent, becoming purplish at maturity, about 4 mm. high and 5–6 mm. broad.

MEXICO. Oaxaca: Zempoaltepetl, top of the mountain, *W. H. Camp 2659*, Sheet I, Feb. 19–27, 1937 (type, N. Y.).

The extreme forms (as *Camp 2659*, Sheet II, pars, in Herb. N. Y. Bot. Gard.) with their small, nearly oval (occasional suborbicular) leaves less than 2 cm. long, might be thought as distinct "species" were forms not found connecting them with more typical plants. These unusual plants, in general, are the result of aerial growth at the tips of long, fast-growing, rhizomatous branches.

Gaultheria Conzattii may be distinguished (*ex descr.*) from the recently described Oaxacan species *G. Cummingii* Sleumer at least by its subcordate or rounded leaf bases. In this connection it is to be mentioned that in his notes (Notizbl. **12:** 125. 1934) Sleumer compares his species with "*G. parviflora*" Small. Judging only by the description, this is an error for *G. parvifolia* Small. *G. Conzattii* may further be easily distinguished (*ex descr.*) from the recently described *G. Schiedeana* Sleumer at least by its much shorter leaves, these being only one-half as long as in *G. Schiedeana*. Although Sleumer does not indicate the state of collection, the locality listed (ibid. **12:** 128) would seem to indicate that the type (and only known

specimen) of *G. Schiedeana* came from Vera Cruz. A sufficient quantity of plants of *G. Conzattii* (numbering into the hundreds) have been studied in the field to convince the writer that there are no intergrades between it and the two species mentioned above.

One character is impressive as one studies the specimens of *G. Conzattii.* Here the glands on the tips of the hairs which clothe the inflorescence (an important feature in the ODORATAE) are reduced in size to little more than enlargements of the tip of the hair, or sometimes, absent. The species typically seems to be confined to El Cerro de San Felipe, near the city of Oaxaca. However, on Zempoaltepetl, about 80 kilometers to the east and the highest mountain in the state, it reappears in a form so like the species that it deserves no more than varietal rank. There are, perhaps, some workers who might segregate these as distinct species, but careful study in the field of both the species and its variety lead me to the conclusion that this newly described species with its variety is on the transition between those groups of species which have either glandular or nonglandular trichomes on their inflorescences.

GAULTHERIA PARVIFOLIA Small.

This species would seem to be closely related to the above species and its variety, for it too is apparently a low subcaespitose shrub, but its much narrower, glabrous leaves (I am unable to find more than a few punctations on the base of the mid-vein indicating the one-time presence of any sort of pubescence on the type—*Galeotti 1848*) would seem to be sufficient to separate these forms.

GAULTHERIA DOMINGENSIS Urban and G. SPHAGNICOLA Rich.

In connection with the general problem of the origin and dispersal of this last group of species, it might be mentioned that *G. domingensis* of the Caribbean region is similar to *G. Conzattii* var. *mijorum*, matching it in almost every respect, even to propagating by runners, as *Turckheim 3152* from Santo Domingo would indicate, but differs in having a relatively much larger calyx, a striking feature of this species.

Continuing on around to the Lesser Antilles we come to Guadeloupe which is supposed to be the northernmost limit of *G. sphagnicola*, differing from *G. domingensis* in having a glabrous corolla. I have seen material from Guadeloupe in which the corolla is glabrous, but more recent collections there by H. Stehlé include specimens of which the corollas have some pubescence. These plants are more robust and have larger corollas as well as slightly different leaves, linking them more closely to *G. domingensis* than to *G. sphagnicola*.

It would seem that *G. Conzattii* and its variety *mijorum* is related to *G. domingensis* and its derived species *G. sphagnicola* and that all of them are parts of and derived from that once remarkable distribution of Tertiary floras which extended from southern Mexico across the now almost completely submerged mountain ranges of ancient Antillia[2] and of which we now have left only marginal remnants in the West Indies, southern Mexico, Central America, and northern South America.

In the group of species derived from the more typical ODORATAE the following may be described as new:

Gaultheria tacanensis Camp, sp. nov. Frutex 0.6 m. altus, ramulis glabrescentibus, punctatis (junioribus pubescentibus?); folia ovalia vel rectangulo-ovata, basi subcordata vel rotundata, apice abrupto-acuminata, supra glabra, subtus glabra dense punctata (junioribus pubescenta?), 2.5–5 cm. longa, 1.5–2.5 cm. lata, margine minute serrata; racemi terminales, 4–6 cm. longi; rachis et pedicelli (circ. 4–5 mm. longi) dense albido-puberuli et dense ferrugino-pilosi, eglandulosi; calyx alte 5-lobus, lobis acuminatis circ. 2.5 mm. longis, crispe ferrugino-pilosis; corolla urceolata (rosea), apice manifeste contracta, crispe ferrugino-pilosula, eglandulosa, 5–6 mm. longa; stamina 10, filamentis basin versus dilatatis dense pubescentibus, 2.5 mm. longis, antheris quadricornutulis circ. 1.5 mm. longis; ovarium depresso-globosum pubescens.

Gaultheria tacanensis is apparently a strict to somewhat spreading shrub about 0.6 m. high with punctate, glabrous branches (the punctations indicating an early-deciduous pubescence); leaves elliptic to oblong, basally subcordate or rounded, apically abruptly acuminate to a minute calloused tip, glabrous above, glabrous but densely punctate below (the punctations being the bases of early-deciduous hairs), 2.5–5 cm. long and 1.5–2.5 cm. wide, minutely serrate, the serrations punctate tipped (the punctations being the bases of early-deciduous hairs); petioles thick, 2.4 mm. long; racemes generally several (?) from the uppermost nodes, 4–6 cm. long, many-flowered; rachis and pedicels (about 4–5 mm. long) with a dense minute puberulence and somewhat abundantly ferruginous-villous, eglandular; bracts linear-oblong, 7–10 mm. long, mostly glabrous except for marginal cilia; bracteoles subulate, minutely ciliate and sparsely villous; calyx deeply 5–lobed, cut almost to the receptacle, the lobes lanceolate or narrowly triangular, acuminate, spreading or reflexed at anthesis (when dry), about 2.5 mm. long, abundantly set with crisped, eglandular, ferruginous hairs; calyx at maturity becoming purple-black, its lobes thin and mostly spreading (when dry), scarcely covering the capsule; corolla pink, 5–6 mm. long, urceolate, manifestly contracted at the apex, its lobes ovate, 0.6–0.7 mm. long, covered with crisped, eglandular, ferruginous hairs; stamens 10; filaments about 2.5 mm. long, basally some-

[2] A term used here to indicate that much warped land-mass with its great series of mountain ranges which once extended across the Caribbean area.

what dilated, densely pubescent, particularly in the contracted part; anthers about 1.6 mm. long; ovary depressed-globose, pubescent; mature capsule depressed, 2–2.5 mm. high and 4–5 mm. broad with broad reddish lines on the outer (ventral) carpel walls.

MEXICO. Chiapas: Volcan Tacana, 10,000 ft. elev. *T. MacDougall* (without number), Jan. 16, 1938 (type, N. Y.).

This species, with no near relatives, but seemingly allied to *G. parvifolia* Small, may be easily distinguished from it by its somewhat more deeply cut and loosely villous calyx lobes. Since the type locality is on the boundary between Mexico and Guatemala[3] it seemed desirable to ascertain the exact location of the collection on the mountain, in spite of the fact that the specimen was labeled as having been collected in Chiapas. Mr. MacDougall informs me that, although he ascended from the Mexican side, at the 10,000 ft. elevation, the trail swings close to what he estimates is the boundary, that the species was seen on both sides of the trail, and it is possible that the plant from which the type was collected may have come from either side of the line. For this reason, it seems reasonable to record *Gaultheria tacanensis* from both Mexico and Guatemala.

GAULTHERIA GLANDULIFERA Small, N. Am. Flora **29**: 78. 1914.

Gaultheria poasana Sleumer, Notizbl. **12**: 127. 1934.

With the type specimen of *G. glandulifera* (COSTA RICA. Prov. Alajuela: Volcan Poas, alt. 2500 m., *J. D. Smith 6639*, M. Mart. 1896). and excellent material of the type collection of *G. poasana* (ibid, alt. 2600 m., *J. D. Smith 6631* M. Mart. 1896) both before me, I am unable to discover any specific difference between them, the differential characters pointed out by Sleumer being only those which one might expect on separate individuals of the same species growing at slightly different altitudes and in somewhat different habitats on the same mountain.

GAULTHERIA COSTARICENSIS (Donn. Smith) Small.

Closely matching the type of this species is the following collection: PANAMA. Forest of Cerro de Lino, above El Boquete, Chiriqui, altitude 1300 to 1560 meters, *H. Pittier 3032*, March 5, 1911. The range of the species is thus enlarged from Costa Rica to Panama.

[3] Although, on most maps, Volcan Tacana is placed in Guatemala, a more recent 1:500,000 scale edition [Estados Unidos Mexicanos. Secretaria de Agricultura y Fomento, Direccion de Estuidos Geograficos y Climatologicos. Hoja "TAPACHULA" (15°–91° 30′). Edición 1932] places the mountain on the international boundary approximately 30 kilometers NNE of Tapachula, Chiapas, with an elevation of 4000 meters.

PERNETTYA

Having a small series of numbers of *Pernettya* to identify, I attempted to make use of the recent monograph of this genus by Sleumer (Notizbl. **12**: 626–655. 1935) but found it inadequate for the specimens at hand. The material was evidently not conspecific and since Sleumer admitted but one species of the genus in Mexico, it was thought best to examine the Mexican material available.

One important factor in a study of this genus is its distribution. Specimens are rarely found below 6000 ft. elevation, reaching their maximum abundance between 8–10,000 feet. They are thus limited to the higher mountains (mainly the slopes of isolated peaks), a potent factor in the development of local endemism. The following treatment of the genus *Pernettya* in Mexico therefore represents my ideas concerning the distribution and speciation of this genus, based to a certain extent on field studies as well as on specimens not available to Sleumer during his revision.

PERNETTYA CILIATA (Cham. & Schlecht.) Small.

Under this species Sleumer has placed all the Mexican material of the genus. In his notes he mentions that the type (*Schiede 268* from the slopes of Orizaba, which I have not seen) is closely similar to *P. Pentlandii* of South America (*P. prostrata* var. *Pentlandii* (DC.) Sleumer, a combination with which I am not in full accord). This statement is further corroboration with my opinion that, if the specific lines are carefully drawn in strict accord with the type concept, *P. ciliata* is not particularly widespread in Mexico.

Specimens from the region around Orizaba closely fit the original description (Linnaea **5**: 126. 1830). Typically their branches are loosely setose; the leaves ovate-lanceolate and glabrous except for a few hairs on the mid-rib, the margins serrate, the serrations stipitate-glandular or occasionally with a few setae. The hairs on the pedicels are crisped and the bracts and sepals are glabrous except for the finely ciliate margins. The corollas and other floral parts, while differing in this from others of the more closely related species, are scarcely diagnostic.

MEXICO. Vera Cruz: "Pied d'Orizaba," *Galeotti 1828;* Orizaba, *Müller* without number in "1855";[4] *Müller 1424*, Aug. 1853;[5] "Malpays

[4] The date on the label is in error. Müller disappeared late in 1853 or early in 1854. 1855 is the year in which Schlumberger distributed the Müller specimens.

[5] This is a transposed label reading "*Arbutus xalapensis* HBK." The number is therefore probably incorrect. Although without locality data I have not hesitated to place the collection in the state of Vera Cruz (and probably near Orizaba) for Müller was known to have collected mainly between Vera Cruz and Orizaba.

de la Joya," *Schiede 171*. Hidalgo: Pine forests near Trinidad Iron Works, *Pringle 8962;* Sierra de Pachuca, *Pringle 11011*.

The specimens cited under *Schiede 171* and *Pringle 8962*, although apparently more robust and with a few of the basal leaves tending to be obovate, have the pubescence of the typical material on Orizaba. The material from Orizaba almost exactly matches the figure and description of *Arbutus pilosa* Graham (*P. pilosa* Don), in Bot. Mag. pl. *3177*.

Pernettya hirsuta (Mart. & Gal.) Camp, Comb. nov.

Gaultheria hirsuta Mart. & Gal. Bull. Acad. Brux. **9:** 540. 1842.

This species, ignored by the recent writers on the Ericaceae either under *Pernettya* or *Gaultheria*, is closely related to the foregoing but may be distinguished from it by the following features:

Branches densely setose; leaves (their margins serrate and completely setose) narrower and basally cuneate, their lower surfaces abundantly setose, the hairs not being limited to the mid-vein as in the preceding.

MEXICO. Oaxaca: "Sierra Pelado," 7000 ft., *Galeotti 1817*, Nov–April, 1840 (cotype of *G. hirsuta*). Vera Cruz(?): *Müller 1499*, August, 1853, without locality (see footnote #5).

It is unfortunate that I have been unable to study additional material of the type collection of this species, some of which came from the Cerro de San Felipe, just north of Oaxaca, but the description and specimen available match so exactly that I do not hesitate to connect our specimen with it. It is further unfortunate that no exact locality can be assigned to *Müller 1499*, cited above. However, it is so different in aspect from the others of his collections cited under a previous species, that the present writer feels certain that it is distinct from them. This and the foregoing species will be further discussed under a later note in this paper.

PERNETTYA BUXIFOLIA Mart. & Gal.

In regard to this species it is interesting to note that Martens and Galeotti recognized the genus *Pernettya*, describing a single species ("*Pernettia buxifolia*," Bull. Acad. Brux. **9:** 538. 1842); that they knew and differentiated the species *ciliata* and *hirsuta*, but on subsequent pages placed them in the genus *Gaultheria* (*loc. cit.* **9:** 539, 540). Here again, although I have not seen the type, the description is reasonably clear and the species may be distinguished from the preceding two by the following characters:

Entire plant, except for an almost microscopic puberulence on the branches, completely glabrous; leaves narrowly elliptic or sometimes linear, with the marginal setae completely absent and replaced by short glands; the pedicellary bracts apparently more reduced and the pedicels

relatively more elongate than in the preceding species. The type apparently was collected in the state of Hidalgo.

MEXICO. Est. Mexico: On Popocatepetl, *Rose and Hay 6047*. Federal District: Serrania de Ajusco, 10,000 ft., *Pringle 6304*.

Thus, with the valid names which have been assigned to Mexican species linked with describable entities and some of the material as yet neither disposed of nor assigned to them, it becomes necessary to describe the following new species.

Pernettya mexicana Camp, sp. nov.

Frutiusculus erectus ad 0.3 m. altus, ramis strigosis; folia angusto-elliptica vel linearia 1.5–2.5 cm. long, 3–6 mm. lata, brevissime petiolata, apice acuta vel obtusa, basi acuta vel subcuneata, subcoriacea, glabra, supra nitida, subtus pallida, margine serrulata (serraturis subacutis minute glandulosis); flores axillares solitarii ad summos ramulorum digesti, pedicellis sparse et crispe pilosis circ. 4–7 mm. longis, bracteae glabrae margine ciliatae; corolla cylindrico-urceolata, alba vel rosea, glabra, circ. 5.5 mm. longa et 4 mm. diam., apice breviter 5-lobata; sepala lanceolata acuminata, circ. 3 mm. longa, glabra, margine ciliata basin glandulosa; stamina 10, 3.5–4.5 mm. longa, antheris breviter 4-aristatis, filamentis glabris basi dilatatis subcarnosis; ovarium elongato-globosum, glabrum, stylo glabro; bacca purpureo-nigrescens.

The strigose branches and narrow, completely glabrous leaves of *P. mexicana* are diagnostic. In this species—and its close relatives—the setae on the leaf-margins are completely absent, being replaced with thickened gland-hairs only 0.15–0.25 mm. long. These marginal glands are homologous with and similar to those on the margins of the sepals—in this species apparently confined to the lower part of these organs.

MEXICO. Oaxaca: Top of Zempoaltepetl, *W. H. Camp 2652*, Feb. 19–27, 1937 (type, N. Y.); Cerro de San Felipe, *Camp 2604;* ibid., "Sierra" de San Felipe, *Pringle 4643*. Puebla: Rio Frio, *Lyonnet 208*. Mexico: Crucero Agua Blanca, *Hinton 4927*, *8325*. Michoacan: Mountains near Patzcuaro, *Pringle 4115*.

Pernettya obovata Camp, sp. nov.

Frutex erectus plus quam 0.3 m. altus, ramis sparse strigosis; folia caulis principalis late cuneata, ramorum floriferum anguste ovalia vel cuneata, glabra, supra nitida, subtus pallida, margine serrulata (serraturis minute glandulosis), petiolo 1–2 mm. longo; rami terminales et laterales flores 8–15 gerentes; flores axillares solitarii, pedicellis crispe pilosis circ. 9–13 mm. longis, bractea glabra margine ciliata et glandulosa; corolla urceolata, glabra, circ. 5 mm. longa et 4 mm. diam., apice breviter 5-lobata; sepala lanceolata acuminata circ. 2.5 mm. longa, glabra, margine ciliata, glandulosa; stamina

10, circ. 3 mm. longa, antheris breviter (0.5 mm.) 4-aristatis, filamentis glabris basi dilatatis; ovarium globosum, glabrum, stylo glabro.

P. obovata is a shrub, coarse for the genus as it occurs in Mexico. Its broader, cuneate, heteromorphic leaves, floriferous branches, glandular bracts and markedly glandular sepals serve to separate it from the preceding.

MEXICO. Oaxaca: Cumbre de Huehuetlân, Distrito de Teotitlan, *C. Conzatti 4112*, May 22, 1921 (type, N. Y.).

Pernettya Tomasii Camp, sp. nov.

Frutex erectus, ramis strigosis; folia elliptica 1.5–2.5 cm. longa, 0.7–1 cm. lata, petiolo 1–2 mm. longo, apice acuta vel obtusa, basi obtusa, subcoriacea, supra glabra et nitida, subtus pallida (costa sparse hirsuta), margine serrulata (serraturis minute glandulosis); flores axillares solitarii, pedicellis circ. 2 mm. longis glandulo-pubescentibus, multibracteatis, bractea glabra margine subciliata; corolla cylindro-urceolata, glabra, circ. 6.5 mm. longa et 4 mm. diam., apice 5-lobata (lobis 1.0–1.5 mm. longis); sepala lanceolata circ. 3.5 mm. longa, margine subciliata et subglandulosa; stamina 10, circ. 3.5 mm. longa, antheris breviter 4-aristatis, thecis divergentibus, basi submucronulatis, filamentis glabris basi dilatatis; ovarium globosum, stylo glabro.

MEXICO. Chiapas: Volcan Tacana, alt. 8–9000 ft., *T. MacDougall* (without number) Jan. 15, 1938 (type, N. Y.); ibid. alt, 8,000 ft. (also at 12,000 ft.[6]), *T. MacDougall*, Jan. 15, 1938.

P. Tomasii, among the Mexican species of the genus, stands unique in having relatively short pedicels at anthesis, the flowers appearing almost sessile. Its nearest relative (and from which it probably is a derivative) is *P. coriacea* Klotzsch of Costa Rica and Panama. It may be distinguished from this last by its thinner leaves, divergent and mucronulate anther sacs, and its shorter pedicels. In *P. Tomasii* the pedicels are about 2 mm. long at anthesis and 3–5 mm. long in fruit, whereas in *P. coriacea* they are 5–8 mm. long at anthesis and 6–12 mm. long in fruit. It may easily be distinguished from the broad-leaved forms of *P. ciliata* by the strigose type of pubescence on its branches. The species is named in honor of the collector of the type, known to our mutual Mexican acquaintances as Don Tomás.

KEY TO THE MEXICAN SPECIES OF PERNETTYA

Flowers subsessile, the pedicels obscured by bracts at anthesis.................... *P. Tomasii.*
Flowers manifestly pedicellate, the pedicels not obscured by bracts at anthesis.
  Branches obscurely puberulent.. *P. buxifolia.*

[6] See footnote #3 and discussion under *Gaultheria tacanensis.* Its presence at this altitude would seem to indicate that the plant also occurs in Guatemala.

Branches strigose or setose.
  Branches setose; leaves hirsute below, at least along the mid-vein.
    Leaves sparsely hirsute, the hairs only on the mid-vein below, margin occasionally setose .... *P. ciliata.*
    Leaves abundantly hirsute below, margin completely setose.......... *P. hirsuta.*
  Branches strigose; leaves glabrous.
    Leaves essentially isomorphic on the same plant, narrowly elliptic to linear.......... *P. mexicana.*
    Leaves heteromorphic, broadly cuneate on the main stem and narrowly oval to cuneate on the flowering branches.......... *P. obovata.*

A NEW HYBRID

A most puzzling form collected near Oaxaca and not referable either to *Gaultheria* or *Pernettya* may be treated as follows:

X Gaulthettya Camp, (*Gaultheria* × *Pernettya*) hybr. gen. nov.

Frutex parvus. Folia alterna coriacea. Inflorescentiae axillares, bracteosae, uniflorae. Pedicelli circ. 10-bracteati, bracteis coriaceis persistentibus. Calyx 5-lobus. Corolla urceolata, apice manifeste contracta, minute lobata. Stamina 10 receptaculo inserta. Filamenta libra, elongata, basin dilatata et carnosa, apice pubescentia. Antherae dorsifixae; thecis 4-aristatis. Discus 10-cornutulus. Ovarium superum, globosum, 5-loculare. Stylus teres, elongatus, inclusus.

X Gaulthettya oaxacana Camp, hyb. sp. nov. (*Gaultheria Conzattii* Camp × *Pernettya mexicana* Camp).

Frutex subcaespitosus ad 0.2 m. altus, ramis dense setosis; folia oblongo-elliptica circ. 2.5 cm. longa et 1 cm. lata, apice acuta, basi rotundata, subcoriacea, supra nitida sparse setosa, subtus pallida ± dense setosa, margine minute serrulata, setosa, petiolo 1–2 mm. longo; flores axillares solitarii ad summos ramulorum digesti, pedicellis dense et crispe pilosis 5–8 mm. longis, bractea sparse villosa, margine glandulo-setosa; corolla globo-urceolata, rosea, sparse hirsuta, circ. 7 mm. longa et 6 mm. diam., apice contracta et 5-lobata, lobis circ. 2.5 mm. longis; calyx 5-lobus, lobis circ. 3 mm. longis, glabris, margine ciliatis; stamina 10, filamentis circ. 2.5 mm. longis, basi dilatatis et carnosis, apice sparse pubescentibus, antheris circ. 1.5 mm. longis; ovarium globosum puberulum; stylus glaber.

The specimens were taken from plants just coming into flower and fairly abundant over an area not less than 10 meters in diameter. The plants appeared to be a clone. The inflorescence characters, as well as the shape and texture of the pedicellary bracts, would closely link them with *Pernettya*, whereas the shape of the corolla, structure of the calyx, pubescence of the staminal filaments, as well as the foliage and general aspect would link them with *Gaultheria*. The finding of occasional abnormal corollas on the type collection would seem to add further credence to the view of its hybrid origin.

MEXICO. Oaxaca: Cerro de San Felipe, upper slopes, *W. H. Camp 2414*, Dec. 29, 1936 (type, hybrid gen. and sp., N. Y.).

The problem of the relationship and origin of the *Gaultheria—Pernettya* complex is again opened up by the finding of this hybrid material. If the two parents had not been growing on the same mountain, and on the same slope nearby, there would have been some hesitancy on the part of the writer in placing it in a hybrid category. Otherwise, it would have seemed sufficiently distinct from either to be described as a new genus.

In Mexico the species of *Gaultheria* known to the writer, although belonging to several species groups, have a certain amount of pubescence on the staminal filaments, their inflorescences are racemose and the calyces are obviously synsepalous. On the other hand, the species of *Pernettya* have glabrous filaments, each branch of the multibracteate inflorescence is reduced to a single flower and the sepals are free nearly to the base and, when carefully examined, are seen to be basally imbricate. In the field, the aspect of the plants is adequate to separate the genera.

However, other features must be considered when attempting to sort the material from South America and the Australian Region. Possibly *Pernettya* could be united with *Gaultheria* but it is more probable that future critical study in this group will lead to the segregation of several additional genera.

In addition to the general interest in this obvious hybrid, it is further important in the interpretation of several of the species of *Pernettya* in Mexico. The bulk of the material of this genus may be characterized as having strigose hairs on the branches, whereas in *Gaultheria*, when a coarse pubescence is present, it is generally of a setose nature (although the hairs are often tipped with glands). However, in two species of *Pernettya*, the branches are setose rather than strigose. These two species are *Pernettya ciliata* and *P. hirsuta*. Careful examination of the material available of both would lead the present writer to the view that it is highly probable that they are the result either of a backcross between such a hybrid as *X Gaulthettya oaxacana* and the *Pernettya* parent, or genetic segration from the hybrid itself.

Of the two, *P. ciliata* seems to be by far the most stabilized and well on its way to becoming established as a species. On the contrary, it is altogether possible that *P. hirsuta*, while a distinct entity, is not a "good species" but serves only as the receptacle into which certain of the extreme pernettyoid segregates can be placed for the sake of present nomenclatorial convenience. The exact status of such forms will never be completely understood until we know the genetics of such hybrids and their segregates.

In conclusion, it may be stated that I am absolutely opposed to maintaining the Mexican species of *Pernettya* under *P. ciliata*, first, because the bulk of the material is not conspecific with it and, second, that this species, in all probability, is not a direct phylogenetic derivative from within *Pernettya*, but carries a certain amount of *Gaultheria* heredity, acquired subsequent to the segregation of the genus *Pernettya* from the ancestral gaultherioid stock.

THE NEW YORK BOTANICAL GARDEN

Additions to Florida Fungi—I

William A. Murrill

(with three figures)

This series will include new species and notes on interesting fungi that are picked up from time to time in Florida. Numbers cited refer to collections in the herbarium of the Florida Agricultural Experiment Station, at Gainesville. Already, about two hundred Florida novelties have either been published or are soon to appear in this and other periodicals. The field is a fertile one, largely unworked.

Agaricus Rhoadsii sp. nov.

Pileo truncato-conico ad expanso, 6.5 cm. lato, fibrilloso-squamuloso, pallide vinoso, disco castaneo; sporis 5×3 μ, stipite albo, bulboso, 8×0.6–1 cm.; annulo amplo, persistente.

Pileus truncate-conic to expanded, solitary, about 6.5 cm. broad; surface dry, finely fibrillose-squamulose, pale dilute-vinosous, castaneous on the flat disk; margin white, sterile, widely projecting, appendiculate and fringed; context firm, white, unchanging, odorless; lamellae free, narrow, inserted, crowded, entire, whitish to dull-pink and finally purplish-brown; spores ovoid, smooth, 1-guttulate, purplish-brown, about 5×3 μ; cystidia none; stipe tapering upward, smooth, white, glabrous, bulbous, 8×0.6–1 cm.; veil very large, membranous, fixed, apical, persistent, double, smooth and white above, decorated with isabelline scales below.

Type collected by A. S. Rhoads and W. A. Murrill under oaks in a high hammock at Gainesville, Fla., Sept. 7, 1938 (*F 18117*). The color is very unusual for the genus, being pale-purple while the flesh is still firm and milk-white. *Lepiota* was at first suggested but the truncate cap was more like *Agaricus*. I know of no other species that approaches it.

Agaricus Weberianus sp. nov.

Pileo convexo-expanso, 7.5 cm. lato, roseo-avellaneo, disco badio, squamuloso; lamellis remotis, sporis ellipsoideis, 5×3 μ; stipite albo, 8×1 cm., annulo amplo, albo, persistente.

Pileus convex to expanded, solitary, 7.5 cm. broad; surface dry, rosy-avellaneous, badious on the smooth broad convex disk, decorated with small flat imbricate scales; margin very narrowly sterile, even, entire to slightly undulate; context thick at the center, white, unchanging, sweet, odorless; lamellae free, remote, narrow, crowded, inserted, entire, pallid to purplish-brown; spores ellipsoid, smooth, purplish-brown, 1-guttulate, about 5×3 μ; stipe equal above the slightly enlarged base, smooth, white, glabrous, 8×1 cm.; veil double, very ample, very thin, white, fixed 1 cm. from the apex, with small isabelline scales on the lower side, hanging 2 cm. long like a wet skirt.

Type collected by W. A. Murrill on a shaded trash pile in Gainesville, Fla., Sept. 9, 1938 (*F 18131*). Suggesting *A. subrufescens* Peck but solitary and having much smaller spores. Dedicated to Dr. George F. Weber, who has taken an active interest in building up our mycological collection.

Pluteus nigrolineatus sp. nov.

Pileo convexo-subexpanso, 2.5 cm. lato, griseo, nigro-reticulato; sporis ovoideis, 8×6 μ, stipite albo, 4×0.4 cm.

Pileus convex to subexpanded, solitary, 2–2.5 cm. broad; surface dry, shining, griseous, with distinct reticulating black lines, margin splitting with age; context very thin, white, odorless; lamellae free, very broad and rounded, inserted, crowded, entire, white to pink; spores ovoid, strongly tapering below, smooth, pink, usually 1-guttulate, about 8×6 μ; cystidia fusoid, truncate, hyaline, about 45×15 μ; stipe subequal, smooth, white, glabrous, shining, the base slightly enlarged, black-lined, partly white and partly dark-blue, 4×0.4 cm.

Type collected by W. A. Murrill on an oak log in Gainesville, Fla., Sept. 8, 1938 (*F 18103*). Suggesting *P. fibrillosus* Murr. but differing in color and microscopic characters. Reticulate as in *P. admirabilis* Peck but having the stipe black-lined at the base.

Pluteus Rhoadsii sp. nov.

Pileo hemisphaerico ad subexpanso, 3–4 cm. lato, scabro, striato, umbrino; sporis subglobosis, 5 μ, stipite albo, glabro, 5–6×0.2–0.4 cm.

Pileus hemispheric to subexpanded, densely gregarious to subcespitose, about 3–4 cm. broad; surface dry, scabrous or hispid, checked at the center, very finely striate, umbrinous, at times fulvous on the disk; margin entire, rimose with age; context firm, white, unchanging, odorless, sweet and nutty; lamellae free, rounded behind, arcuate, narrow, crowded, inserted, white, entire, thick; spores subglobose, smooth, uniguttulate, pink, about 5 μ; cystidia none; stipe enlarged and usually slightly bulbous below, smooth, white, glabrous, fistulose, umbrinous and finely tomentose at the base, about 5–6×0.2–0.4 cm.

Type collected by A. S. Rhoads and W. A. Murrill on a rotten oak log under oaks at the Tung-oil Mill, Alachua Co., Fla., Sept. 7, 1938 (*F 18101*). Suggesting *P. fibrillosus* Murrill, but densely gregarious and having smaller spores.

Venenarius Rhoadsii sp. nov.

Pileo convexo-subexpanso, 5–8 cm. lato, albo, spinuloso; sporis elongatis, 10×14 μ, stipite radicato, volva veloque evanescentibus.

Pileus convex to subexpanded, gregarious, 5–8 cm. broad; surface dry, white, cremeous on drying, decorated with long, pointed warts, especially on

the disk, margin entire, even; context white, unchanging, with strong odor of chloride of lime; lamellae adnexed with decurrent ridges, rather broad, medium distant, inserted, entire, white, becoming brown when dried; spores sausage-shaped, smooth, hyaline, about 10×4 μ; stipe white, floccose-squamose, cremeous when dry, about 5×1–1.5 cm., the root 5–10 cm. long, either elongate-fusiform or elongate-turbinate; veil white, breaking up into floccose fragments; volva soon disintegrating and mostly carried up on the cap.

Type collected by A. S. Rhoads under live-oak at Lake Rosa, Putnam Co., Fla., Sept. 8, 1938 (*F 18125*). Suggesting *V. solitariiformis* Murrill but having a strong odor of chloride of lime.

Armillaria Boryana (Mont.) Murrill, comb. nov.

Collybia Boryana Sacc. Syll. Fung. **5**: 240. 1887.

This tropical American species is frequent about Gainesville on oak logs and stumps, often appearing in quantity, but the presence of a veil was not noticed until Mr. Erdman West brought in a collection he made at Magnesia Springs, Fla., July 3, 1938 (*F 17344*). In young hymenophores about 1.5 cm. broad, the tough, white, membranous veil had just ruptured from the stipe, exposing the young gills in a polygonal area. Older hymenophores showed broad fragments of the veil attached to the margin, while in still older stages hardly a trace of the veil was left. At no time was an annulus present, the stipe being simply squamose where a ring might have been.

Appearing here in the same season with the above, also on the tops of hardwood logs in woods, is another interesting tropical species, *Armillaria alphitophylla* (Berk. & Curt.) Murr., described from the Bonin Islands and noted for its immense spores and cystidia. In some specimens the caps are as spotted as the skin of a leopard.

Lactaria subtestacea sp. nov.

Pileo convexo-depresso, 7 cm. lato, viscido, testaceo-ochraceo, piperato; lamellis ochroleucis, sporis globosis, tuberculatis, 6 μ; stipite glabro, ochroleuco 5×1.7–2 cm.

Pileus convex to slightly depressed, solitary, 7 cm. broad; surface viscid, indistinctly striate, not at all zonate, uniformly testaceous-ochraceous, shining, margin entire, concolorous; context pallid, opaque, unchanging, odorless, slowly distinctly acrid; lamellae adnate, medium broad, medium distant, 3–4-times inserted, entire, ochroleucous; latex white, unchanging; spores globose, distinctly tuberculate, hyaline, 1-guttulate, about 6 μ; stipe equal, uneven but not pitted, glabrous, pale rosy-ochroleucous, 5×1.7–2 cm.

Type collected by W. A. Murrill on the ground in a high hammock at

Gainesville, Fla., Sept. 21, 1938 (*F 18209*). An attractive species without near relatives and doubtless very rare.

Galactopus serifluus sp. nov.

Pileo convexo-subexpanso, umbilicato, 1.5 cm. lato, melleo, disco subnigro; lamellis adnatis, albis, sporis ovoideis, 3×2 μ, stipite 2×0.2 cm.

Pileus convex to subexpanded, umbilicate, gregarious, 1.5 cm. broad; surface smooth, glabrous, opaque, melleous, blackish at the center; margin incurved, even, entire; context rather thick, opaque, pallid, odorless, somewhat mawkish, bleeding watery drops when cut; lamellae adnate with a small decurrent tooth, medium distant, broad behind, inserted, entire, white, unchanging; spores ovoid, smooth, hyaline, 1-guttulate, about 3×2 μ; cystidia none; stipe equal, smooth, pallid and pruinose above, subconcolorous and subglabrous below, whitish-tomentose at the base, 2×0.2 cm.

Type collected by W. A. Murrill on a rotten magnolia log in a hammock at Gainesville, Fla., Sept. 14, 1938 (*F 18104*). An aberrant species with incurved margin like *Gymnopus* and bleeding from the context more than from other parts of the hymenophore. Dried specimens would be referred to *Gymnopus* without hesitation. *Galactopus rugosodiscus* (Peck) Murr. is probably its nearest relative.

Gymnopus albidus sp. nov.

Pileo convexo-expanso, 1.5–2 cm. lato, albo; lamellis sinuatis, albis, sporis 10×4 μ, stipite pellucido, 3×0.1–0.3 cm.

Pileus convex to plane or umbilicate, gregarious to subcespitose, 1.5 to 2 cm. broad; surface smooth, glabrous, uniformly white, margin even, entire; context thin, white, unchanging, odorless, mild; lamellae sinuate, rather crowded, broad, ventricose, inserted, entire, white, unchanging; spores pip-shaped, smooth, hyaline, granular, about 10×4 μ; cystidia none; stipe equal, smooth, glabrous, translucent, 3×0.1–0.3 cm.

Type collected by E. West and W. A. Murrill in soil at the base of a southern red cedar at Magnesia Springs, Fla., Sept. 17, 1938 (*F 18176*). A white species growing in soil and having a translucent stipe.

Gymnopus palmarum sp. nov.

Pileo hemisphaerico, 4–6 mm. lato, testaceo, farinaceo; lamellis albis, sporis 4–5×3 μ, stipite testaceo, 2×0.1–0.2 cm.

Pileus conic to hemispheric, not expanding, gregarious to cespitose, 4–6 mm. broad; surface dry, testaceous, finely fibrillose-tomentose; margin even, entire, sharply incurved when young; context thick at the center, thinning out toward the margin, pale yellowish, taste decidedly farinaceous; lamellae adnate, broad, inserted, distant, entire, white to discolored; spores ellipsoid,

smooth, hyaline, granular, 4–5×3 μ; cystidia few, hyaline, long, gradually tapering to a sharp point; stipe cartilaginous, equal or unequal, smooth, shining, glabrous, testaceous, hollow, about 2×0.1–0.2 cm.

Type collected by W. A. Murrill in soil about the base of a Washington palm in Gainesville, Fla., Sept. 7, 1938 (*F 18102*). A small species with hemispheric, testaceous cap and shining stipe. It has no near relatives.

Gyroporus umbrinisquamosus sp. nov.

Pileo convexo, 6 cm. lato, isabellino, umbrino-squamuloso, sapore grato; tubulis parvis, albidis, sporis albis, 9–11×4–5 μ; stipite praeclavato, 6×1.3–2 cm.

Pileus broadly convex, solitary, 6 cm. broad; surface dry, isabelline, with conspicuous umbrinous fibrillose squamules, margin entire, even; context about 5 mm. thick, white, unchanging, mild, odorless; tubes plane, depressed, about 5 mm. long, mouths minute, circular, not stuffed, white with a faint sulfur tint, unchanging; spores oblong-ellipsoid, obliquely apiculate, granular, smooth, hyaline, about 9–11×4–5 μ; stipe very clavate, hollow, pubescent, dull-rosy-isabelline above, umbrinous below, 6×1.3–2 cm.

Type collected by W. A. Murrill on the ground in turkey-oak woods at Gainesville, Fla., September 2, 1938 (*F 17417*). Suggesting *Tylopilus peralbidus* (Snell & Beard.) Murrill, but squamulose and not bitter.

Poria Rhoadsii sp. nov.

Late effuso, adnato, 6–12×2–4 cm., margine albo, fimbriato; tubulis flavis ad roseo-avellaneis, 3–5×0.3 mm., sporis hyalinis, 2×1 μ.

Widely effused, adnate, uneven, following the irregularities of the substratum in patches 2–4 cm. wide and 6–12 cm. long; margin narrow, thin, white, fimbriate, more or less evanescent; sterile zone back of extreme margin thicker and flavous, remaining flavous in dried specimens; context hardly apparent at maturity; tubes irregular, angular, quite firm, flavous within and without, 3–5 mm. long, about 3 to a mm., edges thick to thin, becoming dentate, changing from flavous to pale-roseous with age, distinctly rosy-avellaneous when dry, presenting a pleasing contrast to the younger flavous tubes; spores ellipsoid, smooth, hyaline, 2×1 μ; cystidia none.

Type collected by A. S. Rhoads and W. A. Murrill on a decorticated sweet-gum log in a high hammock north of Hunter's Station, Fla., Sept. 6, 1938 (*F 18132*). Also collected by West and Murrill on a decayed log at Gainesville, Fla., Sept. 16, 1932 (*F 9111*). A beautiful species, which I tried hard to connect with *P. vitellina* (Schw.) Cooke. The spores cited above fell on a glass slip under a bell-jar. They seem rather small. Others found floating about in section mounts were ellipsoid, smooth, hyaline,

1-guttulate, 8×4–5 μ. These seem much too large to be basidiospores of such a plant.

Inonotus ludovicianus melleus var. nov.

Pileo melleo, zonato, tubulis non constipatis, sporis 5×3 μ.

Pileus finely hispid-tomentose, slightly sulcate, melleous, concentrically banded with umbrinous-melleous zones about 1 cm. broad; context soft-corky, pallid to umbrinous, about 1 cm. thick; hymenium stramineous at the sterile border, avelaneous where the young tubes have formed, and umbrinous behind; tubes 2–3 mm. long, about 3 to a mm., angular, entire, not stuffed when young; spores ellipsoid, obliquely apiculate, granular, pale-ferruginous under the microscope, about 5×3 μ.

Type collected by West and Murrill on the base of a living laurel oak at Magnesia Springs, Fla., Sept. 17, 1938 (*F 18177*). A splendid variety, reaching 22×32 cm., honey-yellow banded with darker zones, the tubes not stuffed when young, and the spores somewhat smaller than in the typical form. The species no doubt causes considerable decay in oak trees.

Ganoderma Curtisii (Berk.) Murrill

Described from South Carolina in 1849 and known to occur from New York to Florida and Texas on living and dead trunks, stumps, or roots

Fig. 1. *Ganoderma Curtisii* (Berk.) Murrill ×⅙. Hymenophore on trunk of living ash at Gainesville, Fla. Photo by G. F. Weber.

of oak, sweet gum, maple and certain other deciduous trees. The accompanying illustration is from a photograph taken by Dr. G. F. Weber on living ash, an unusual host. I have observed the development of this particuiar specimen for some time. The species is very abundant about Gainesville, especially on oaks, and it undoubtedly does considerable damage.

Fig. 2. *Ganoderma sulcatum* Murrill $\times \frac{1}{4}$. Hymenophore on dead trunk of *Butia capitata* Becc. at Gainesville, Fla. Photo by G. F. Weber.

Those who have studied the rot describe it as very striking and distinct. There is much work yet to be done, however, before our knowledge of the species of *Ganoderma* and the injury caused by them is anything like complete.

GANODERMA SULCATUM Murrill

Described from Florida in 1902 and known to occur there commonly on palmetto trunks and logs. In September, 1938, it was found at Gainesville on a small "*Cocos australis*" (*Butia capitata* Becc.), which had died in less than a year from transplating. The hymenophore measured 6×9 inches and was about three inches thick behind. The following notes on the decay are contributed by Dr. G. F. Weber, plant pathologist in the Florida Agricultural Experiment Station.

"The palm was dug and sectioned and it was found that the root sys-

tem and lower portion of the main trunk, although slightly discolored, was not infected by the fungus. A cross-section 18 inches up from the butt end (this cut being below the position of the sporophore) showed occasional mycelial infected pockets, mostly in the center of the trunk. Another section, just above the sporophore, showed elongated pockets from the center to the edge; the largest, lenticular in shape, 1×2 inches, and the smallest,

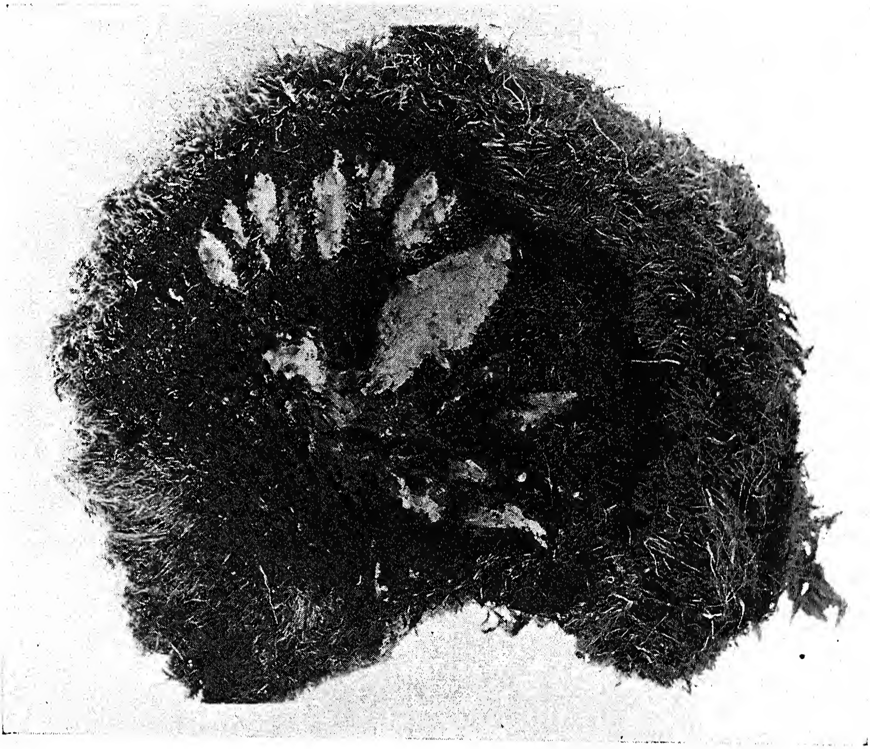

Fig. 3. Cross section of trunk of *Butia* showing decayed wood with mycelium of *G. sulcatum*. Photo by G. F. Weber.

elongate. Other sections toward the top of the plant showed that these pockets increased in number and size until they reached the growing point of the palm, which was in a putrescent condition. The lower extremities of the pockets in the wood were surrounded by dark chocolate-brown color, which apparently showed the advance of the fungus beyond which point no mycelium was found. The base of the leaf petioles showed an accumulation of mycelium next to the trunk. The fungus probably invaded the palm through the upper portion, which was suffering because of transplating operations, and was advancing toward the base. It probably did

not kill the palm but it is evident that it was a material factor in the disintegration and decay of the main trunk."

NEW COMBINATIONS

For those using Saccardo's nomenclature the following new combinations are made:

Galactopus serifluus = **Mycena seriflua**
Gymnopus albidus = **Collybia albida**
Gymnopus palmarum = **Collybia palmarum**
Gyroporus umbrinisquamosus = **Boletus umbrinisquamosus**
Venenarius Rhoadsii = **Amanita Rhoadsii**

HERB. FLA. AG. EXP. STATION
GAINESVILLE, FLORIDA

New Ferns from Bolivia and Peru[1]

WILLIAM R. MAXON AND C. V. MORTON

(WITH ONE FIGURE)

In the course of zoological field work in Bolivia in 1926, under the auspices of the American Museum of Natural History, Mr. G. H. H. Tate made a considerable botanical collection, which was turned over to the New York Botanical Garden. The ferns and fern allies (about 250 numbers) were subsequently sent to U.S. National Museum for identification. A considerable number of them are from comparatively low elevations and represent rather common or widely distributed species, but those from the higher mountains are of decided interest, since they include such rarities as *Cheilanthes andina* Hook., *Diplazium mapiriense* Rosenst., and *Lycopodium pendulinum* Hook., besides the new species herewith described. In addition, there are several critical forms in *Elaphoglossum*, *Polystichum*, and *Struthiopteris*, which, though apparently new, it seems inexpedient to describe at present in view of existing confusion within these genera.

There are included descriptions of a second new species of *Blechnum* collected in Bolivia by Prof. M. Cárdenas and a new *Polypodium* from Peru, the latter being represented in the Tate collection by a sterile specimen only.

Polypodium megalolepis Maxon & Morton, sp. nov.

§ *Lepicystis*, venatione *Goniophlebii*. Rhizoma rampans, paleis planis imbricatis castaneis concoloribus ovato-attenuatis magnis (usque ad 10 mm. longis) subpersistentibus laxe onustum. Folia pauca, remota, stipitibus tenuibus quam laminis plerumque paulum brevioribus; lamina oblonga vel deltoideo-ovata, usque ad 11 cm. longa et 6 cm. lata, profunde pinnatifida; laciniae 7-jugae, subaequales vel superiores infra apicem elongatum subabrupte reductae, lineares, late et longe decurrentes, dense opacae (marginibus conspicue callosis obtuse serrulatis), subtus subremote punctato-paleaceae, paleis minutis, rotundis vel maximis (1 mm. longis) late ovatis et abrupte attenuatis, castaneis, marginibus erosis pallidioribus; areolae obliquae, ellipticae, magnae, uniseriales, 8–12-jugae; sori 7–11-jugi, rotundi, 3–4 mm. diam., mediales, fere paginam inferam totam tegentes.

Epiphytic, the rhizome rampant, lightly attached at intervals, more than 30 cm. long, flattish in drying, 3–4 mm. broad (excluding scales), densely but loosely imbricate-paleaceous, the scales laxly oblique, ovate-attenuate, very large, 8–10 mm. long, 2–3 mm. broad, attached at sinus of deeply cordate base (basal lobes rounded and widely over-lapping, often elongate), lightly denticulate, plane, firm, castaneous, concolorous, nearly uniform in structure, not

[1] Published by permission of the Secretary of the Smithsonian Institution.

clathrate, the cells very small, variable in shape, irregularly oblong or linear, with outer and partition walls of similarly pale coloration, or those near point of attachment shorter, with thicker partition walls. Fronds few, conform, about 4 cm. apart, 14–18 cm. long, the stipe somewhat shorter than the blade, dull castaneous, 1 mm. thick, bisulcate ventrally, nearly naked; blades oblong to deltoid-ovate, 10–11 cm. long, 4–6 cm. broad, deeply pinnatifid, the rachis broadly alate, concealed; segments about 7 pairs, oblique-spreading, their width apart at middle, subequal or the upper ones reduced below the subconform elongate apex, linear, up to 4 cm. long and 7 mm. broad at middle, acuminate, broadly decurrent, the basal ones extending 1–1.5 cm. downward upon the stipe; veins oblique, 8–12 pairs, goniophlebioid, the single row of large elliptical areoles reaching three-fourths the distance to the margin, with a few excurrent branches; sori 7–11 pairs, superficial, medial, round, 3–4 mm. broad, adjacent, confluent at maturity, non-paraphysate, the sporangia very numerous. Leaf tissue rigidly thick-coriaceous, opaque, yellowish-green, the strongly cartilaginous margins bluntly serrulate; upper surface of segments naked; lower surface persistently punctate-paleaceous, the scales not contiguous, mostly roundish and about 0.5 mm. broad, the largest ones roundish-ovate and abruptly acuminate-attenuate, all the scales appressed, dark castaneous with pale erose margins.

Type in the U. S. National Herbarium, no. 604,470, collected in the Lucumayo Valley, Peru, June 18, 1915, by O. F. Cook and G. B. Gilbert (no. 1283).

Not only in general appearance but in technical characters *P. megalolepis* differs from previously described species too widely to require detailed comparison. The long-decurrent segments are an outstanding character; also the very large, laxly imbricate, concolorous rhizome scales, these not at all reticulate or clathrate, but of fine nearly uniform cellular structure, the cells being minute and elongate with the outer walls colored like the thin partition walls.

This species is known also from Bolivia, from a sterile specimen (herb. N. Y. Botanical Garden) collected at Alaska Mine, alt. 4110 meters, March 1926, by G. H. H. Tate (no. 54).

Blechnum malacothrix Maxon & Morton, sp. nov.

Rhizoma ut videtur suberectum, ca. 1.5 mm. diam., paleis ovatis appressis fuscis crassis lucidis minutis praeditum. Folia plura, fasciculata, erecta, 10–25 cm. longa, stipitibus tenuibus quadrangularibus stramineis, laminas subaequantibus, tristelicis, glanduloso-pilosulis; lamina linearis, sursum attenuata, 5–14 cm. longa, usque ad 2.6 cm. lata, basi pinnata, sursum pinnatisecta, rhachi subdense glanduloso-pilosula; laciniae 12–20-jugae, infimae distantes, paulum reductae et reflexae, subauriculatae, superiores

anguste oblongae (maximae 12.5 mm. longae et 4.5 mm. latae), patentes, antrorse subfalcatae, apice rotundae, basi late adnatae, antice auriculatae, marginibus leviter callosis, scabridis; coenosori ca. 1 cm. longi et 2 mm. lati, crassi, indusio glabro, manifeste inframediali, angusto; parenchyma herbacea, utrinque dense glanduloso-pilosa.

Rhizome (incomplete) short, oblique, 1.5 mm. thick, appressed-paleaceous; scales narrowly ovate, deeply cordate, 0.5–0.8 mm. long, shining, blackish (central cells opaque, the basal ones irregularly hexagonal, the distal elongate, the marginal pale and translucent), bearing a few distant cilia. Fronds several, fasciculate, erect, 10–25 cm. long, the stipes tristelar, stramineous, quadrangular, very slender (about 0.5 mm. in diam.), 6.5–12 cm. long, sparsely paleaceous near base, rather densely glandular-pilosulous, the hairs 3- to 5-celled, up to 0.5 mm. long; blades linear, attenuate in apical half, pinnate at base, above pinnatisect nearly to the subcaudate apex; rachis densely glandular-pilose; pinnae 12–20 pairs, opposite or alternate, the lowest 8–12 mm. distant, slightly reduced, subreflexed, the middle ones narrowly oblong, up to 12.5 mm. long and 4.5 mm. wide, spreading almost horizontally, upwardly subfalcate, rounded at apex, broadly adnate, auriculate distally, the lower pinnae slightly auriculate basally also; margins lightly cartilaginous, scabrous; leaf tissue herbaceous, densely glandular-pilose on both surfaces; coenosori about 1 cm. long, 2 mm. wide, very thick, the indusia distinctly inframedial, distant about 0.5 mm. from the midrib, narrow, glabrous; sporangia very numerous; annulus 13-articulate; spores reniform, about 35 μ long, pale yellow.

Type in the New York Botanical Garden, collected at Okara, Cordillera Real, Bolivia, altitude 2250 meters, April 26–29, 1926, by G. H. H. Tate (no. 951). Duplicate in the U. S. National Herbarium.

The relationship of *B. malacothrix* is doubtless with *B. laevigatum* Cav., of which *B. distans* Presl is a synonym, as is probably also *B. Juergensii* Rosenst. The two differ as follows:

Blade linear; segments not more than 4.5 mm. wide, rounded at apex; stipe, rachis, costae, and leaf surface densely glandular-hairy; rhizome scales minute, the central portion blackish, opaque. *B. malacothrix.*

Blade triangular-lanceolate or lanceolate; segments 5–10 mm. wide, mucronate at apex; stipe, rachis, costae, and leaf surface sparsely glandular-hairy; rhizome scales larger, concolorous, brown, the cells all translucent . . . . *B. laevigatum.*

Blechnum delicatum Maxon & Morton, sp. nov.

Rhizoma suberectum, ca. 2 mm. diam., paleis paucis deltoideo-lanceolatis acuminatis firmis fusco-castaneis brunneo-marginatis usque ad 1.5 mm. longis onustum. Folia plura, fasciculata, 9–15 cm. longa, stipitibus 1–5.5 cm. longis,

Fig. 1. *Polypodium megalolepis* Maxon & Morton.
The type specimen; about half natural size.

tenuibus, bistelicis, stramineis, glanduloso-pilosulis, basi paleas brunneas paucas majusculas ferentibus; lamina anguste linearis, 5–12 cm. longa, basi pinnata, supra subpinnatisecta, utrinque attenuata, apice elongato integro; rhachis ubique glanduloso-pilosula, epaleacea; laciniae 13–26-jugae, infimae subdistantes, rotundae, adnatae, superiores leviter conjunctae, late triangulares, usque ad 6 mm. longae, integrae, apice rotundo mucronulatae, costa subflexuosa obscura; venae paucae; coenosori usque ad 4 mm. longi, indusio glabro manifeste inframediali; parenchyma membranaceo-herbacea, supra subglabra, subtus minute glanduloso-pilosula.

Rhizome suberect, about 2 mm. thick, sparingly paleaceous, the scales triangular-lanceolate, acuminate, 1–1.5 mm. long, thick, opaque, very dark castaneous, the margins pale brown, translucent, bearing a few capillary teeth. Fronds fasciculate, numerous, ascending, 9–15 cm. long, the stipes subimbricate, 1–5.5 cm. long, about 0.5 mm. thick, bistelar, stramineous, terete, sulcate ventrally, glandular-pilosulous, sparingly paleaceous at base, the scales pale brown, translucent, otherwise like those of the rhizome; blades linear, 5–12 cm. long, 7–13 mm. broad, pinnate at very base, subpinnatisect upwardly, attenuate both ways, the apex elongate (1–1.5 cm.), entire; rachis glandular-pilosulous, devoid of scales; segments 13–26 pairs, the lower 1 to 3 pairs subdistant, rounded, 2.5–3 mm. long, 4–5 mm. broad, wholly adnate at base, the other segments all faintly joined, broadly triangular, up to 6 mm. long and 5 mm. wide, entire, rounded and slightly mucronate at apex, the costa very obscure, subflexuous; lateral veins about 4 pairs, the lower ones furcate; leaf tissue delicately herbaceous, nearly glabrous above, minutely glandular-pilosulous beneath; coenosori up to 4 mm. long and 2 mm. wide, the indusia conspicuously inframedial, glabrous; annulus about 14-articulate; spores reniform.

Type in the U. S. National Herbarium, no. 1,618,695, collected at Roboré, Bolivia, altitude 416 meters, October 1934, by M. Cárdenas (no. 3006).

The alliance of this species is clearly with *Blechnum asplenioides* Sw., which it resembles habitally and in its small size, basally attenuate blades, and adnate segments. The two may be distinguished as follows:

Stipes slender, glandular-pilosulous; rachis and leaf tissue glandular-pilosulous; segments slightly longer than broad, rounded and mucronulate at apex; veins 4 pairs .... *B. delicatum*

Stipes shorter and stouter, glabrous; rachis and leaf tissue glabrous, thicker; segments obviously longer than broad, acute or acuminate; veins about 6 pairs .... *B. asplenioides.*

Struthiopteris brasiliensis (Raddi) Maxon & Morton, comb. nov.

Lomaria brasiliensis Raddi, Pl. Bras. **1**: 50. *pl. 72, 72 bis.* 1825.

Blechnum Raddianum Rosenst. Hedwigia **46:** 91. 1906.

This species has not previously been recorded from Bolivia. It was collected at Okara, alt. 2250 meters, Apr. 26–29, 1926, by Tate (no. 938), and at Sirupaya, Yungas, alt. 2250 meters, by Buchtien (no. 467). The latter was determined by Rosenstock as *Blechnum capense* (L.) Schlecht., an Old World species.

Struthiopteris Buchtienii (Rosenst.) Maxon & Morton, comb. nov.

Blechnum Buchtienii Rosenst. Repert. Sp. Nov. Fedde **5:** 231. 1908.

Founded on *Buchtien* 878, from Unduavi, northern Yungas, and apparently not uncommon in Bolivia at elevations of 3000 to 4000 meters, e.g. *Tate* 357, from Cocopunco. In Peru Señor C. Bües found it at Cerro Colca, Valle de Lares, alt. 4000 meters (no. 1878), and it is reported also from Ecuador. Among Bolivian species it is readily distinguished by the long, stiff, linear scales of the caudex.

Struthiopteris penna-marina (Poir.) Maxon & Morton, comb. nov.

Polypodium penna-marinum Poir. in Lam. Encycl. **5:** 520. 1804.

Blechnum penna-marinum Kuhn, Fil. Afr. 92. 1868.

This characteristic species is chiefly antarctic in distribution, but has been collected several times in Bolivia at high elevations (3000–3900 meters). Mr. Tate found it at Pongo (nos. 118, 119, 844).

Dicranopteris boliviensis Maxon & Morton, sp. nov.

Rhizoma repens, minute tuberculatum, paleis rigide ciliatis castaneo-fuscescentibus elongato-deltoideis nitentibus crassis 3–4 mm. longis deciduis onustum. Folia erecta, umbraculiformia; stipes 50 cm. longus, castaneo-fuscescens, basi tuberculatus, glabrescens; lamina suborbicularis, ca. 20 cm. longa et lata, 4- vel 5-dichotoma, numquam trichotoma, axibus medialibus abortivis, gemmis inclusis dense paleaceis, internodiis 3.5–1.5 cm. longis, nudis, vel ultimis 2–4 segmenta parva interdum ferentibus; pinnae lineares, usque ad 16 cm. longae et 1.5 cm. latae, subpinnatisectae, costis paleis laxe ciliatis castaneis elongatis praeditis; laciniae pruinatae, lineares, acutae, basi connata 3 mm. latae, sursum vix 2 mm. latae, rigide herbaceo-coriaceae, concavae, marginibus valde revolutis, costulis laxe fibrilloso-paleaceis; venae paucae, prominulae supra; sori mediales, sporangiis ca. 4 formati.

Plants small. Rhizome wide-creeping, 3 mm. in diameter, bluntly tuberculate (tubercles 0.5–1 mm. long), deciduously paleaceous; scales 3–4 mm. long, 1 mm. broad, narrowly triangular from a rounded base, attenuate, very dark castaneous, thick, rigidly ciliate. Fronds erect, umbraculiform; stipe 50 cm. long, 3 mm. thick, very dark castaneous, deciduously scurfy, tuberculate at base, not extended as a primary axis; blades about 20 cm. long and broad, 4 or 5 times dichotomous, the included buds (with a single exception) dormant,

not producing minor axes; internodes about 3.5 cm., 2.5 cm., 1.5 cm., and 1.5 cm. long respectively, diverging at an angle of about 60°, naked, or the ultimate ones bearing 2–4 reduced segments on the inner side; buds relatively large, the closely imbricate scales similar to those of the rhizome but thinner, paler, and bearing numerous very long, lax, whitish cilia; pinnae narrowly linear, 8–16 cm. long, 8–15 mm. broad, long-attenuate, very deeply pinnatifid throughout or sometimes naked a distance of about 1 cm. at outer base; rachises persistently paleaceous, the scales similar to those of the buds, spreading, 1.5–2 mm. long, laxly ciliate; segments numerous (35–50 pairs), slightly oblique, linear, 5–9 mm. long, 3 mm. broad at base, concave (the margins strongly revolute), 1.5–2 mm. broad at middle, acute, the costule elevated beneath, fibrillose-paleaceous, a few fibrils extending to the veins; veins 9–11 pairs, mostly once-forked, evident above; immersed beneath; sori medial, mostly 4-sporangiate. Leaf tissue rigidly herbaceo-coriaceous, strongly pruinose beneath.

Type in herbarium of the New York Botanical Garden, collected at Cocopunco, Cordillera Real, Bolivia, alt. 3000 meters, March 24–29, 1926, by G. H. H. Tate (no. 351). Duplicate in U. S. National Herbarium.

In architecture, especially in the non-development of primary and minor axes from the included buds of the dichotomies, *D. boliviensis* somewhat suggests *D. rubiginosa* (Mett.) Maxon, of Colombia and Venezuela, in miniature. That species differs greatly otherwise in having the primary branches only once or twice dichotomous, the first internodes naked or partially pectinate, the second internodes often fully pectinate, and the rachises clothed with fulvous or ferruginous, rigidly ciliate scales, the cilia ferruginous or often darker.

United States National Museum
Washington, D. C.

On the Genus Cyclodium[1]

C. V. Morton

The South American fern genus *Cyclodium* has not had quite as varied a nomenclatural history as most genera of the tribe Dryopterideae. Since its establishment by Presl[2] in 1836 it has almost invariably been recognized as valid, except by Hooker and Baker, who reduced it to a section of *Aspidium*. Presl distinguished his genus from *Nephrodium* by its anastomosing venation and orbicular, peltate indusium. He cited three species: *C. glandulosum* (founded on *Aspidium glandulosum* Blume), *C. confertum* (founded on *Aspidium confertum* Kaulf.), and *C. meniscioides* (founded on *Aspidium meniscioides* Willd.). Inasmuch as the first of these has a reniform indusium, attached at the sinus, it can not be taken as the type of the genus. The Willdenow species has rightly been taken as the type, that of Kaulfuss having usually been regarded as a synonym.

Considering Presl's tendency to multiply genera and the limited number of species known to him, *Cyclodium* must be considered as having been relatively well founded. It may be doubted, however, if recent fern students have carefully considered its claims to generic standing. During a study of certain recent collections it became apparent to me that a proper distinction from *Dryopteris* is lacking, and in order to clarify the following discussion I give here a brief summary of the important characters of *Cyclodium*.

It is a fern with imparipinnate fronds of papery or subcoriaceous texture, with alternate subentire pinnae. The lateral veins are numerous and almost straight, and spread at a broad angle. The four to six pairs of secondary veins diverge at an acute angle and anastomose with the opposing vein. The two united veins then go out in an excurrent veinlet, which may or may not be united with the next succeeding pair of veins; and this is the type of venation that has come to be known as meniscioid. The sori arise in two rows between the lateral veins, being borne on the secondary veins about midway between origin and point of anastomosis. They are rotund, and possess an orbicular, centrally attached, subcoriaceous indusium. In the variety *conferta* the fertile pinnae are contracted and the sporangia often cover the under surface, but in typical *C. meniscioides* this is not true. The blades of both are glabrous throughout, sparsely paleaceous, and conspicuously pellucid-punctate. The outermost vein-branches are united throughout and do not reach the margin.

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[2] Tent. Pterid. 85. 1836.

The venation just described can not be considered as separating *Cyclodium* from *Dryopteris*. Indeed, this type of venation is most typically developed in *Dryopteris*, where it is found in three different subgenera: *Meniscium*, *Goniopteris*, and *Stigmatopteris*. There is nothing unusual about the sori, except the circular indusium and its peltate attachment, but these too are found in subgenus *Stigmatopteris*, section *Peltochlaena*.

The following characters are enumerated by Christensen[3] as distinguishing *Stigmatopteris:* (1) The sporangium in falling is loosened from its pedicel, which remains fixed to the receptacle. This is true also in *Cyclodium*, but may not be a very important character. (2) The veins never reach the margin and often anatomose. (3) All species are entirely glabrous but more or less paleaceous. (4) The lamina is pellucid-punctate. (5) The pinnae terminate in a sharply serrate apex. This is not true in *Cyclodium*, but can hardly be considered a generic character. (6) The apex is pinnatifid. The blades are imparipinnate in *Cyclodium*. This can not be considered a generic criterion, since imparipinnate blades are characteristic of *Dryopteris*, subgenera *Meniscium* and *Goniopteris*, sect. *Eugoniopteris*.

Thus it is seen that there is no important difference whatever between *Cyclodium* and *Stigmatopteris*. The latter is now recognized by Christensen as generically distinct from *Dryopteris*. In such a usage, however, the name itself is invalidated by *Peltochlaena* Fée, validly published for a species now included in *Stigmatopteris*. One solution of the problem would be to unite these two genera in one, under the older name, *Cyclodium*, characterized by the peltate indusium and glabrous pellucid-punctate blade, with veins not reaching the margin. However, such an aggregation of species would be highly unnatural. Already *Stigmatopteris* as recognized by Christensen includes a number of anomalous species, such as *S. opaca* (*Dryopteris Christii*), *S. varians*, and *S. guianensis* (*Dryopteris subobliquata*), that are certainly not very closely related to *S. rotundata* or *S. caudata*, or others of the principal group of species. The further inclusion of *Cyclodium menisci-oides* would render the group entirely artificial, and it is not here suggested that *Cyclodium* is phylogenetically very close to such a species as *Stigmatopteris rotundata*. In fact, it seems likely that in origin *Cyclodium* is closer to *Goniopteris* or *Meniscium*. However, as a matter of convenience, it may be referred to *Dryopteris* subgenus *Stigmatopteris*, since, as pointed out, that subgenus is already a heterogeneous assemblage.

The reduction of *Cyclodium* to *Dryopteris* is not new here. That was done in 1891 by Otto Kuntze; but inasmuch as he gave no discussion of the matter, his views have been ignored.

[3] Bot. Tidskr. **29**: 292–294. 1909.

The following key to those species of *Stigmatopteris* with peltate indusia and anastomosing veins is offered. This is an artificial grouping. In fact, *D. clypeata* may not properly be included in *Stigmatopteris* at all, because of the presence of hairs. It is an anomalous species of uncertain relationship, but shows in gross form a certain similarity to *Cyclodium meniscioides*.

KEY TO SPECIES

Blades pinnatifid at apex, i.e. without a conform terminal pinna.
  Pinnae sharply serrate to the acuminate apex; basal veinlets anastomosing.....1. *D. varians*.
  Pinnae lightly crenulate; basal anterior venule free (venation subgoniophlebioid) 2. *D. calophylla*.
Blades imparipinnate, the terminal pinna conform; venation meniscioid.
  Costae and veins glabrous beneath, somewhat paleaceous; areoles 4–6-seriate; pinnae acute or short-acuminate.
    Pinnae strongly ascending, the sterile not over 9 cm. long and 2.1 cm. broad, finely and evenly serrulate almost to base..3. *D. paludosa*.
    Pinnae patent, the sterile 13–25 cm. long and 4–8 cm. broad, subentire to lightly undulate.
      Blades nearly conform, the fertile 11–17 cm. long, 2.5–4 cm. broad, the sporangia never confluent over the surface, the margin subentire or irregularly sinuate-crenate 4. *D. meniscioides*.
      Blades subdimorphic, i.e. the fertile pinnae contracted, not over 10 cm. long and 1.5 cm. broad, the sporangia numerous and more or less covering the surface, the margins usually deeply and regularly crenate throughout...4a. *D. meniscioides* var. *conferta*.
  Costae and veins beneath puberulous, not paleaceous; areoles 14–17-seriate; pinnae cuspidate-acuminate..5. *D. clypeata*.

1. Dryopteris varians (Fée) Kuntze, Rev. Gen. **2:** 814. 1891.
Nephrodium varians Fée, Mém. Foug. **11:** 88. *pl. 24, fig. 2*. 1866.
Dryopteris varians Kuntze, Rev. Gen. **2:** 814. 1891.
Stigmatopteris varians Alston, Kew Bull. Misc. Inf. **1932:** 309. 1932.

This rare species was described from Trinidad, from which locality I have examined two specimens, one from the Trinidad Botanic Gardens Herbarium (no. 1225) and one collected on border of forest stream at Aripo Savanna by N. L. and E. G. Britton (no. 2941). Otherwise it is known to me only from the Mazaruni River, British Guiana (*Jenman* in 1899, *de la Cruz* 2880).

2. **Dryopteris calophylla** Morton, sp. nov.

Rhizoma ignotum; frondes fertiles usque ad 1.5 m. altae, steriles latiores ca. 1 m. altae; stipites straminei sulcati glabri, parce paleacei, paleis lineari-lanceolatis glabris atrobrunneis, margine parce fibrillosis; rhachis 63–68 cm. longa straminea glabra, supra sulcata, paleacea, paleis lineari-subulatis subpersistentibus instructa; lamina pinnata sed non imparipinnata, pinnis superioribus gradatim minoribus et in apicem pinnatifidum demum subintegrum reductis; pinnae 15–18-jugae, alternae, fere horizontaliter patentes papyraceae, fere concolores, pallide virides, pellucido-punctatae, lineari-

lanceolatae, maximae ca. 21 cm. longae et 3.5 cm. latae, apice acuminatae sed non caudatae, basi rotundatae, paullo acroscopicae, pinnis majoribus evidenter petiolulatis (usque ad 7 mm.), steriles subintegrae vel leviter crenulatae, fertiles crenatae; costa subtus glabra, straminea paleacea, paleis persistentibus subulatis, saepissime apicem versus cellulis uniseriatis praedita; nervi laterales 40–60-jugi, inter se 3.5–5 mm. distantes, leviter flexuosi vix arcuati, paleis parvis subulatis sparse instructi; venula anterior basalis libera, venulis ceteris (ca. 3) cum oppositis anastomosantibus, venula excurrente saepe cum venula exteriori proxima conjuncta, marginem versus venulis irregulariter anastomosantibus, mesophyllo glabro; sori inter nervos laterales biseriati, alterni, in venulis submediales, receptaculo rotundo non elongato elevato; indusium orbiculare peltatum coriaceum subpersistens glabrum.

Type in the U. S. National Herbarium, nos. 1,662,621–3, collected in the vicinity of Barranca Bermeja, Magdalena Valley, Department of Santander, Colombia, altitude 100–500 meters, Sept. 4, 1934, by Oscar Haught (no. 1353).

3. **Dryopteris paludosa** Morton, sp. nov.

Rhizoma ignotum; rhachis et stipes brunnei sulcati glabri, parce paleacei, paleis mox deciduis lineari-subulatis brunneis clathratis glabris instructi; lamina lineari-lanceolata, sterilis ca. 40 cm. longa, fertilis ca. 50 cm. longa, imparipinnata; pinnae 12-jugae, angulo acuto adscendentes, alternae, fere conformes, oblongo-lanceolatae, usque ad 9 cm. longae et 2.1 cm. latae, chartaceae, apice acutae nunquam acuminatae, basi obtusae, superiores sessiles, inferiores brevissime petiolulatae (ca. 3 mm.), utrinque glaberrimae, costa costulaeque parcissime paleaceae, paleis lineari-subulatis deciduis, margine pinnarum sterilium fere usque ad basin regulariter serrulata, fertilium grosse crenata; nervi primarii 30–40-jugi recti, non arcuati, marginem non attingentes, nervis secundariis 4–6-jugis cum oppositis in venula excurrente anastomosantibus, areolis obliquis inaequilateralibus; sori inter venas biseriati, in venulis saepe mediales, receptaculo rotundato, nunquam elongato, paullo elevato; indusium orbiculare centrale peltatum subcoriaceum persistens glabrum; annulus 16–18-articulatus; sporae reniformes, ca. 60 μ longae et 40 μ latae; paraphyses nullae.

Type in the herbarium of the New York Botanical Garden, collected at Puerto Berrio, Department of Antioquia, Colombia, alt. 130 meters, Jan. 11–13, 1918, by F. W. Pennell (no. 3723).

4. DRYOPTERIS MENISCIOIDES (Willd.) Kuntze, Rev. Gen. **2:** 813. 1891.
Aspidium meniscioides Willd. Sp. Pl. **5:** 218. 1810.
Cyclodium meniscioides Presl, Tent. Pterid. 85. *pl. 2, fig. 20.* 1836.
Nephrodium meniscioides J. Sm. in Hook. Journ. Bot. **4:** 188. 1841.

Soromanes integrifolia Fée, Mém. Foug. **2:** 82. *pl. 42*. 1845, as to sterile frond.

In the Index Filicum *Aspidium heterodon* Schrad.[4] is mentioned as a doubtful synonym, but from the description of the pinnae as sharply serrate at the apex it can hardly be referable here. I have seen the following specimens:

BRITISH GUIANA: Pomeroon River, *de la Cruz* 3119; Bartica, *de la Cruz* 1921; Kamwatta, *de la Cruz* 1177; Demerara River, *Jenman.*

BRAZIL: Tanaii, *Spruce;* Tapaná, near Pará, *Killip & Smith* 30331; without specific locality, *Glocker* 10.

PERU: Puerto Bermudez, Dept. Junín, *Killip & Smith* 26566; Santa Rosa, Dept. Junín, *Killip & Smith* 26165; Pongo de Manseriche, Dept. Loreto, *Mexía* 6193a.

4a. DRYOPTERIS MENISCIOIDES var. **conferta** (Kaulf.) Morton, comb. nov.

Aspidium confertum Kaulf. Enum. 232. 1824.

Cyclodium confertum Presl, Tent. Pterid. 85. 1836.

Nephrodium confertum J. Sm. in Hook. Journ. Bot. **4:** 188. 1841.

Aspidium Hookeri Klotzsch, Linnaea **20:** 364. 1847.

"*Cyrtomium confertum* Presl" ex C. Chr. Ind. Fil. 197. 1905. (Error for *Cyclodium*).

Cyclodium rigidissimum C. Chr. Bot. Tids. **25:** 79. 1902.

Most recent fern students have considered *Aspidium confertum* Kaulf. a synonym of *Cyclodium meniscioides*, but the differences in the fertile pinnae seem to require the recognition of the former as a variety. The sterile blades are indistinguishable. *Aspidium Hookeri* was founded on the plate of *Aspidium confertum* Kaulf. given by Hooker and Greville (Icon. Fil. *pl. 121*. 1829), which was supposed to be different from the original species of Kaulfuss. The two are certainly the same, however, the venation shown in the plate of Hooker and Greville being highly inaccurate. I have examined the following specimens:

VENEZUELA: Lower Orinoco, *Rusby & Squires* 377, 379.

BRITISH GUIANA: Waini River, *de la Cruz* 3844; Amakura River, *de la Cruz* 3488; Assakatta, *de la Cruz* 4302; Penal Settlement, *Hitchcock* 17124; Kangaruma-Potaro Landing, *Gleason* 183; Essequibo River, *Jenman.*

FRENCH GUIANA: Baduel, *Leprieur* 27.

BRAZIL: Tapaná, near Pará, *Killip & Smith* 30316; Pará, *Petelot* s. n.

[4] Goett. Gel. Anz. **1824:** 869.

PERU: Mischuyacu, Dept. Loreto, *Klug* 241.
BOLIVIA: San José, *Williams* 1191.
PARAGUAY: Alto Paraná, *Fiebrig* 6344; Caaguazú, *Hassler* 9049.

5. **Dryopteris clypeata** Maxon & Morton, sp. nov.

Herba terrestris, usque ad 82 cm. alta, frondibus fertilibus quam sterilibus longioribus; rhizoma breviter repens, parce paleaceum; stipites distichi usque ad 48 cm. longi, quam laminae longiores, rubro-brunnei, supra sulcati, glabri, basi paleacei, paleis lanceolatis brunneis clathratis, parce ciliatis, externe parce pilosulis (pilis simplicibus); lamina ovata imparipinnata; pinnae 4 vel 5, alternae, inferiores suboppositae, oblongae conformae, usque ad 22 cm. longae et 8.5 cm. latae, utrinque pallide virides et concolores, nitentes chartaceae, pellucido-punctatae, margine subincrassatae integrae vel leviter undulatae, apice subito cuspidato-acuminatae, superiores late et aequaliter cuneatae, inferiores basi superiori superioribus similes sed basi inferiori usque ad 1 cm. non foliaceae, breviter petiolulatae (3 mm.); costa rubescens puberula epaleacea, nervis lateralibus 30–40-jugis rubescentibus puberulis epaleaceis subrectis, marginem versus paullo arcuatis, marginem attingentibus, inter se 5–6.5 mm. distantibus, venis secundariis 14–17-jugis inter se 2–3 mm. distantibus subrectis vel saepe subsigmoideis, cum venulis oppositis anastomosantibus et in venula excurrente saepe libera prolongatis, mesophyllo glabro; sori inter venas laterales biseriati, submediales, receptaculo rotundo, non elongato, paullo elevato; indusium orbiculare centrale peltatum subcoriaceum subpersistens, margine non ciliatum, superficie parce pilosulum; annulus 17–19-articulatus; sporae reniformes, immaturae 44 μ longae et 21 μ latae; paraphyses nullae.

Type in the U. S. National Herbarium, nos. 679,433–4, collected on hills back of Puerto Obaldía, San Blas Coast, Panama, altitude 50–200 meters, August 1911, by H. Pittier (no. 4309).

UNITED STATES NATIONAL MUSEUM
WASHINGTON, D. C.

INDEX TO AMERICAN BOTANICAL LITERATURE

The aim of this Index is to include all current botanical literature written by Americans, published in America, or based upon American material; the word America being used in the broadest sense.

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The Mechanics of Conidial Fertilization in Neurospora sitophila

MYRON P. BACKUS[1]

(WITH PLATES 1 TO 4 AND ONE FIGURE)

Neurospora sitophila Shear and Dodge is a heterothallic ascomycete with a *Monilia* imperfect stage. Single ascospore isolates have been found to fall into two reaction groups commonly designated as "A" and "B." Although sclerotial bodies (incipient perithecia) may be produced on isolated thalli of both reaction groups, it is only when an A strain is mated with a B strain that mature ascocarps are obtained.

In a paper published in 1932 Dodge (5) described experiments demonstrating that the microconidia produced by *N. sitophila* may act as fertilizing agents. When a suspension of microconidia from one strain was applied to the sclerotial bodies on a plate culture of a strain of the opposite reaction, these incipient perithecia in the localized areas to which microconidia were applied promptly developed into normal perithecia which matured spores. Further experiments made clear that a suspension of ordinary monilioid conidia (macroconidia) could be substituted for the microconidia and that these macroconidia are even more effective as "spermatizing agents." The writer had the privilege of witnessing the above-mentioned experiments and has himself since then many times conidiated plate cultures of *N. sitophila* and watched the remarkably rapid transformation of the sclerotial bodies into perithecia in the conidiated areas (1).

Dodge and Swift (9) suggested that some of the hair-like outgrowths which may be seen protruding from the sclerotial bodies when one looks down on a plate culture with a low-powered microscope, might be receptive hyphae. Later, as a result of study of stained sections of incipient

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perithecia in monosporous cultures of *N. sitophila*, Dodge (6) was able to demonstrate that trichogynous hyphae actually are formed, taking their origin from various cells of the ascogonium. He concludes that "there can be no doubt that when one applies either the orange-colored monilioid conidia or the microconidia artificially, these trichogynous outgrowths are the means by which nuclei of the other sex are brought into the ascogenous cells." The fusion of microconidia or of macroconidia with these extensions from the ascogonium, was, however, never observed.

The present study is an extension of this line of investigation; it has brought to light some further details concerning the mechanism of fertilization in *N. sitophila*. In this work only three strains of the fungus were employed: an albino (non-conidial) "A" strain, "56.6," a conidial "B" strain, "56.4," and a conidial "A" strain, "56.8." These were kindly supplied by Dr. B. O. Dodge. For the pedigree of these races the reader is referred to Dodge's original account (4), pp. 11–13.

THE YOUNG SCLEROTIAL BODY

To study the initial stages in the development of sclerotial bodies, cover glasses were placed directly on the agar surfaces of 48-hour-old plate cultures of strain 56.6. It was thus possible to observe under high magnification the manner in which the incipient perithecium originates and to follow the early stages of its development. The essential points observed in this connection are the following: Each sclerotial body begins as a more or less helically coiled hypha originating from one of the vegetative hyphae of small diameter. The coil soon becomes septate, and from its lower part grow out branches which initiate the sterile covering that comes to consist of a dense intertwining mass of threads.

Microtome sections of fixed material stained in iron-alum haematoxylin revealed the ascogonium to be made up of a short coil of cells of greater diameter than the cells of the envelope and more readily staining. The ascogonium appears to be the terminal part of the original helical outgrowth. The fertile cells are of various sizes, but all are multinucleate. Some of the nuclei of the fertile cells are rather consistently much larger than others, even in the same cell, and both large and small nuclei occasionally show a paired arrangement. Until considerable growth of the sclerotial body has occurred, the fertile coil ends blindly and remains enveloped by the sterile sheath. Only later do trichogynous extensions grow out.

All these observations are in approximate agreement with the account given by Dodge (6).

TRICHOGYNE-CONIDIUM RELATIONS

In an attempt to study the trichogyne system and the relations which, according to Dodge's hypothesis, this system must establish with conidia of the opposite reaction placed upon the agar surface, the conventional approach of sectioning and staining fixed material was first employed. Blocks of agar from marked conidiated areas of plate cultures were fixed at intervals of two hours over a period of approximately two days. Study of this material, however, gave only a fragmentary picture of the trichogynes; and although conidia were recognizable in the finished slides, no spores were seen attached to receptive hyphae. A technique yielding much better results was soon substituted.

It was found that the mycelium of strain 56.6 could be induced to grow across a sterile glass slide placed on the surface of the agar in a petri dish. The inoculum was placed on one side of the dish and the slide directly in the middle. The cultures were incubated at 23°C. and at this temperature not only did the hyphae seem to grow over the slide readily, but formed an abundance of sclerotial bodies there. Test conidiations showed that perithecial development identical with that occurring on agar could be obtained on the surface of the glass. Series of cultures of race 56.6 were therefore started on corn-meal agar. When sclerotial bodies appeared on the mycelium which had grown over the glass, a conidial suspension was prepared from a young culture of strain 56.4. This suspension after being filtered through several layers of sterile filter paper was painted over the surface of the slides with a delicate camel's hair brush. The cultures were then returned to the incubator. At two hours following, slides were removed from the dishes, cotton blue dissolved in lacto-phenol was applied with a pipette, and cover glasses were added. After suitable staining, the excess cotton blue was washed out by drawing clear lacto-phenol under the cover glass by means of a blotter. Preparations so made gave a full picture of the trichogynes and also made clear the associations of these with the conidia introduced. When one examines with a microscope the surface of a young plate culture of *Neurospora* there is no way of distinguishing the trichogynes among the numerous sterile hyphae which grow out from the surface of the sclerotial body at about the same time as the trichogynes. In the cotton blue preparations, however, the differential staining obtained not alone revealed the ascogonium clearly in the young sclerotial body, but also made the trichogynous outgrowths from it stand out so well that they were readily traced throughout their entire extent.

The fully developed trichogyne system of certain sclerotial bodies was found to be remarkably extensive, consisting in some cases of two or three

branching trichogynes arising from several cells of the ascogonium. If, as is occasionally the case, a single trichogyne is present, this appears to be simply an extension from the tip of the ascogonial coil. Instead of a simple prolongation of the coil, however, there may be a forking of the end cell and two trichogynes growing out. A trichogyne may give rise to a branch before leaving the pseudoparenchymatous envelope of the sclerotial body, this branch then apparently burrowing its way to the exterior independently. Each trichogynous branch after emerging from a sclerotial body may in turn send out one or more ramifications. In addition to the extensions from the terminal region there may also be in the more complicated cases a trichogyne arising from the penultimate or antepenultimate cell of the ascogonial coil. Figures 1, 2, and 4 illustrate some of the variations met with. The longest single trichogynous hypha encountered was 750μ long; and the total length of the most extensive trichogyne system—adding up the lengths of all branches—was 2000μ. The trichogynes are in general very slender, have occasional cross walls, and usually taper gradually toward their distal ends. On the whole they are of smaller diameter than the hair-like outgrowths from the superficial cells of the sterile covering of the incipient perithecium or than any other hyphae in the field. Dodge (6) described presumably receptive hyphae growing to the outside from the basal part of the ascogonium. Such hyphae could not be identified in the preparations made as here described.

Probably because of the presence of some inhibiting substance produced in the metabolism of the mycelium, conidia which are placed on the agar or glass surfaces across which hyphae have grown do not germinate. The conidia placed on the glass slides as previously described stain even more intensely than the trichogynes, so that they are readily recognizable, but no signs of germination were observed.

Beginning about 4 hours after conidiation fusions between conidia and trichogynes were evident. Whether it is a matter of trichogynes by chance encountering the conidia, or whether a chemotropic attraction exists which causes the trichogynous branches to seek out, as it were, the conidia, is not clear. Although there is some reason for suspecting a chemotropic response on the part of the trichogynes, the evidence is yet inadequate to justify a definite conclusion. In any case it is primarily terminal portions of the trichogyne which are receptive. Very often the tip of a long trichog-

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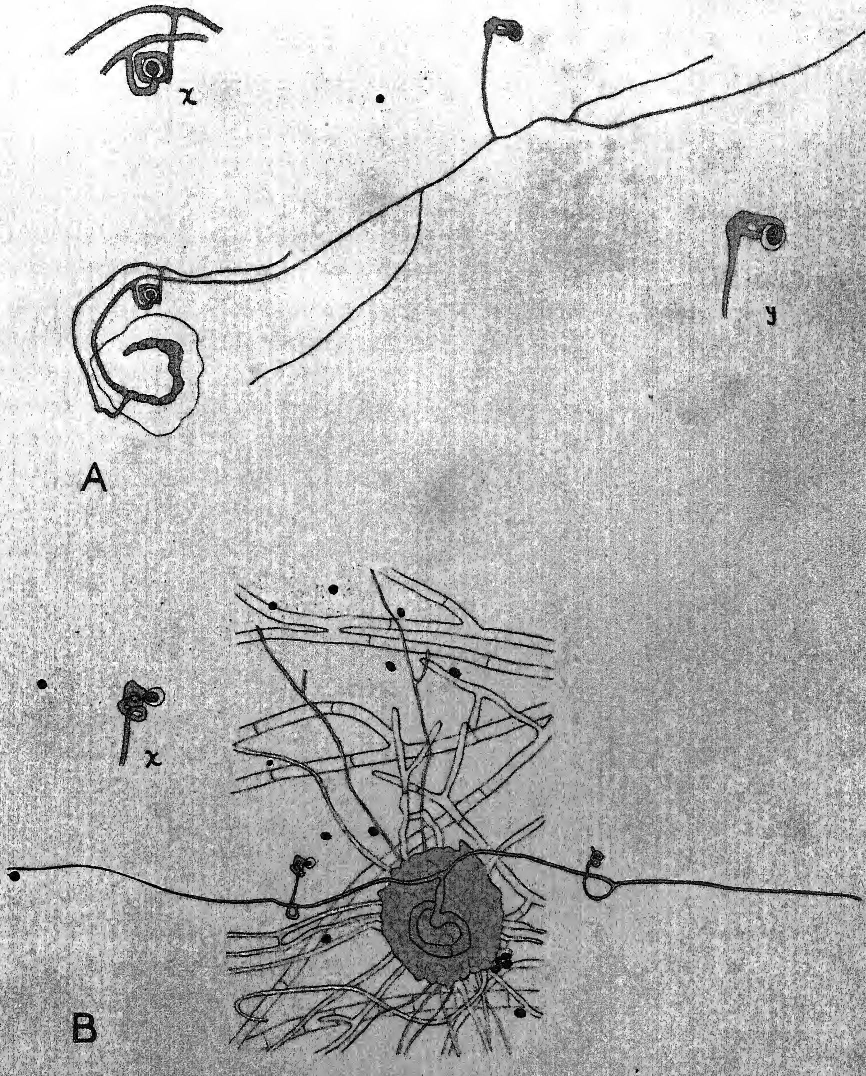
Explanation of Plate 1

Fig. 1. A and B. Trichogyne-conidium relations in *Neurospora sitophila*, nine hours after conidiation. x and y detail of union of trichogynous hyphae with conidia. Camera lucida sketches. Large figures $\times$ 170; x and y $\times$ 340.



BACKUS: NEUROSPORA FIG. 1

thecia induced to form through conidiation contain both "A" and "B" ascospores.

Although in *Neurospora* hyphal fusions are common between vegetative hyphae, and although sterile hyphal outgrowths from the surface of the young perithecium have frequently been seen to fuse with one another or with similar outgrowths from near-by perithecia or even with ordinary vegetative hyphae of the parent culture, no case of fusion of any portion of the trichogyne system with such hyphae has been disclosed by a relatively careful search. Furthermore, in a single trial involving a considerable number of preparations, no evidence was found of union of trichogynes with conidia, when conidia of the same reaction (A) from strain 56.8 were used in conidiating plate cultures of strain 56.6.

In a renewed attempt to study the receptive apparatus in stained sections, thick sections were cut parallel to the surface of the agar. A few preparations were obtained showing a portion of a trichogyne which could be traced back to the fertile coil. Branching and attachment of conidia were seen. These preparations are valuable chiefly in making it clear that the situation observed when the development takes place on a glass surface, is a true picture of what occurs when the fungus is growing on an agar medium.

LOCALIZED DEVELOPMENT OF PERITHECIA

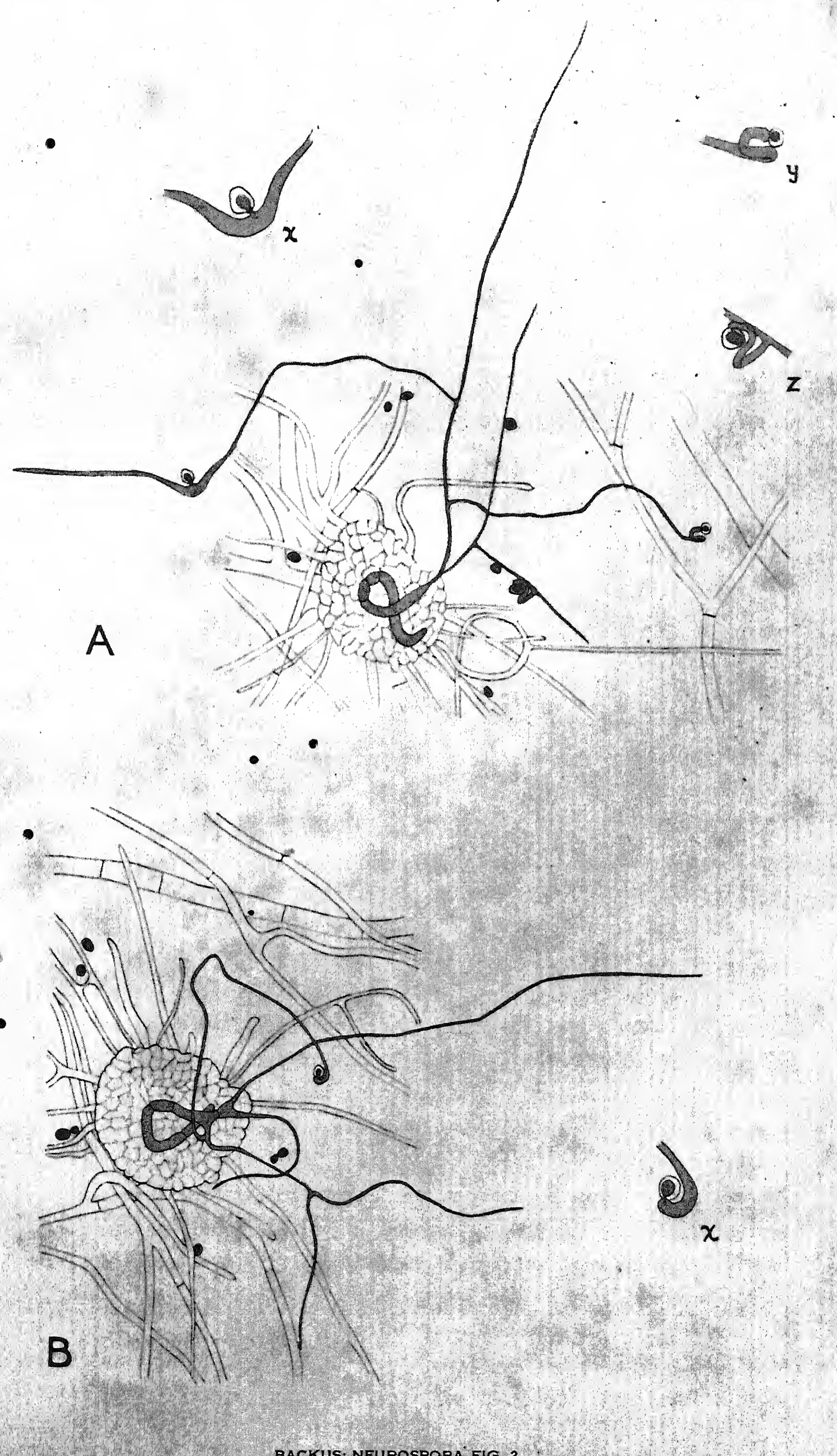
The above account of trichogyne-conidium relations suggests why localized development of perithecia results when conidia of the appropriate reaction are placed on sclerotia-covered areas of *N. sitophila* cultures. Localized development of perithecia may, however, be obtained in a variety of ways. This is evident from the results of the experiments now to be described.

Droplets of a filtered conidial suspension of strain 56.4 were applied to young cultures of strain 56.6 in marked areas wherein the mycelium had grown but where no sclerotial bodies had yet developed. As previously pointed out, conidia do not germinate when placed on areas occupied by mycelium. As soon as sclerotia were formed fertilization was effected; and the same localization of perithecia was obtained as if spores had been placed on sclerotia-bearing regions.

Strain 56.6 is a rapidly growing race. This is important in considering the results of the next experiment. When conidia of strain 56.4 were placed

Explanation of Plate 2

Fig. 2. A and B. Trichogyne-conidium relations in *N. sitophila*, nine hours after conidiation. x, y, and z detail of union of trichogynous hyphae with conidia. Camera lucida sketches. Large figures ×200. x, y, and z ×400.



BACKUS: NEUROSPORA FIG. 2

on the clear agar just a little beyond the advancing margin of the mycelium in a plate culture of strain 56.6, the same localized development of perithecia again occurred—although these bodies appeared only about the third day after conidiation, i.e., after the mycelium had penetrated the area and sclerotia had been formed. Observations made on certain plates following the application of conidia revealed a portion of the spores beginning to germinate. Within a few hours, however, the vigorous hyphae of strain 56.6 had crossed the conidiated area. The presence of the invading hyphae of course made further observation difficult but, in so far as could be seen, growth of germ tubes of strain 56.4 was arrested or at least greatly inhibited. Spores which had not germinated at this stage probably did not germinate at all.

In another experiment fertilization of sclerotial bodies was effected with germinated spores. Conidia of race 56.4 were germinated in a corn-meal decoction. When germ tubes had been produced, droplets of the suspension of germinating spores were applied to areas on plate cultures of strain 56.6 where sclerotial bodies were abundant. Perithecia promptly matured in these areas. The same result was obtained when germinated ascospores from a mating of strain 56.6 (A) and strain 56.4 (B) were used. Ascospores which had been discharged against and caught upon the upper lid of a petri dish were washed into corn-meal decoction and heated in this at 60°C. for 40 minutes to stimulate germination. Presumably approximately 50% of the ascospores applied to the sclerotial bodies on the cultures of strain 56.6 were of the opposite reaction (B). Attempts to observe the germinated spores which had been placed on the culture were relatively unsuccessful. Ascospores could be more easily located than conidia because of their dark walls, but the germ tubes were usually lost in the maze of hyphae about them. In a few instances, however, the germ tubes could be followed; and it is interesting to note that some of them had more than doubled their original length in a period of twelve hours on the culture surface. While it is evident that their growth had been sharply checked, nevertheless at least some germ tubes apparently continued to elongate slowly.

In still another experiment fertilization was effected with mycelial mats. By making a heavy sowing of conidia of strain 56.4 in weak corn-meal decoction in a petri dish, a fine mat of hyphae was obtained which, so far as could be determined, produced no spores of any kind. Small squares of this mat were cut out with fine sterilized scissors and transferred to the surface of cultures of strain 56.6 bearing sclerotial bodies. Many of the sclerotial bodies in the areas to which the mycelial mats were applied enlarged and matured into normal perithecia.

RELATIONS OF TRICHOGYNES AND GERMINATED CONIDIA

Since germinated conidia can bring about fertilization as effectively and promptly as can ungerminated conidia, it seemed desirable to determine the details of the fertilization process. The same technique used earlier in connection with the study of trichogyne-conidium relations was employed. Preparations made *in toto* and stained with cotton blue showed that the receptive portions of a trichogyne upon coming in contact with a germ tube tend to wind about it in a spiral (Fig. 4). Cytoplasmic connections could not be observed, but evidence of gelatinization of trichogynous hyphae near the germ tubes fifteen hours after conidiation suggests that protoplasm of the complementary strain had entered. Frequently a single trichogyne system was found by its ramifications to have come in contact with several germinated conidia (Fig. 4), and more than one trichogyne branch was sometimes found in contact with a single germinated conidium.

FERTILIZATION EXPERIMENTS INVOLVING DEFINITE NUMBERS OF SPORES

Series of experiments were conducted which involved over a hundred plate cultures of strain 56.6 and in which was determined the exact number of spores—ungerminated or germinated—applied to marked areas on the plates.

In approximately 80% of the cases in which a droplet of sterile distilled water containing a single ungerminated conidium of strain 56.4 was placed on a spot at which sclerotial bodies were abundant, or on a spot covered by mycelial growth too young to have formed incipient perithecia, no ascocarps developed. In about 20% of the cases a single perithecium of unusual size matured. When several conidia were present in the droplet applied, a number of perithecia might be formed, but the number of perithecia rarely equaled the number of spores applied (Fig. 5, A–E). An analysis of the results obtained in many trials showed that on an average one perithecium was matured for every four or five conidia introduced.

A different picture appeared when germinated conidia were used. In these tests conidia of race 56.4 each with a germ tube no more than ten times the length of the original conidium were employed. In about 85% of the cases in each of which a single germinated spore was applied, a small

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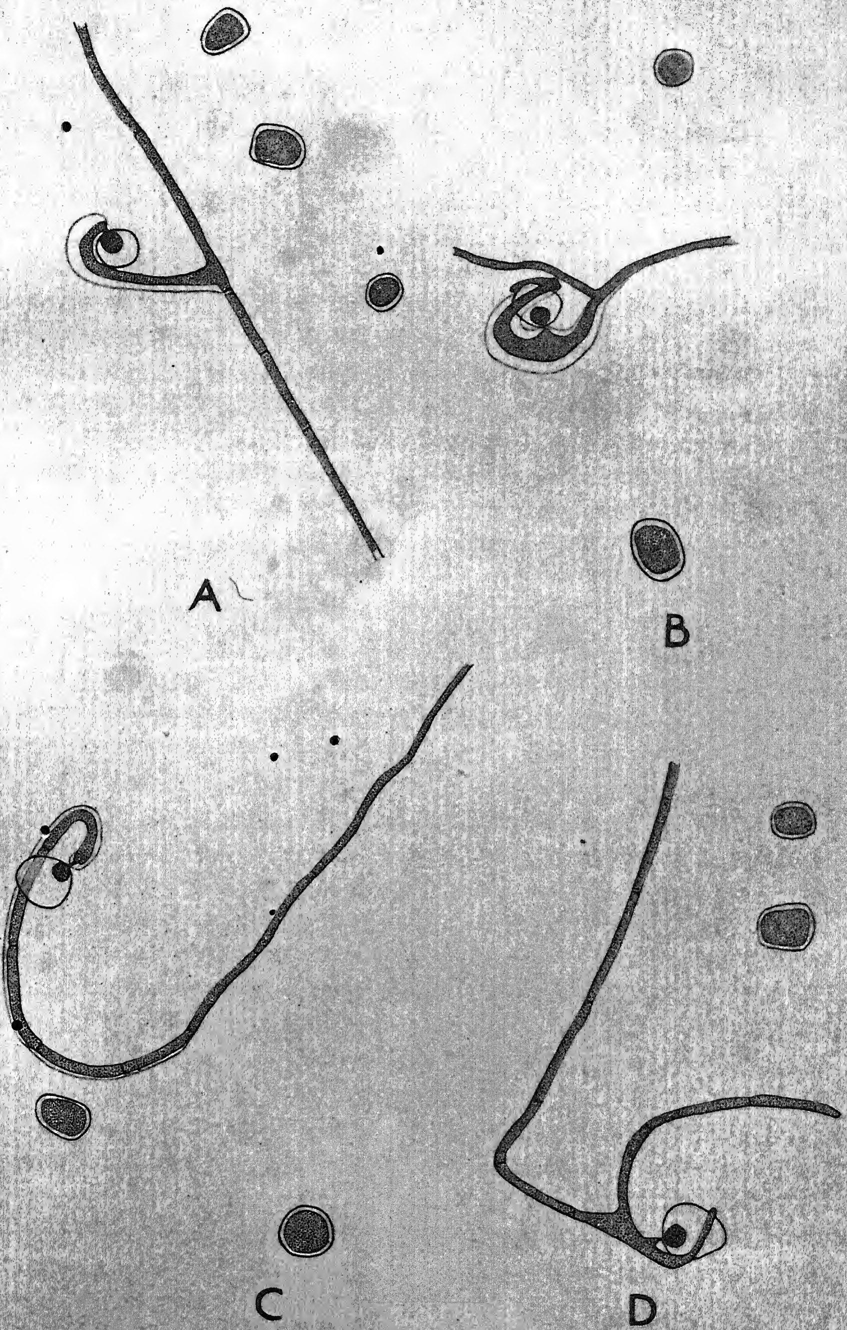
Explanation of Plate 3

Fig. 3. Detail of portions of trichogynous hyphae which have fused with conidia, 12 hours after conidiation. In each case the major part of the protoplasm of the attached conidium has passed into the trichogyne. Unattached conidia from the same fields are also shown. ×750.



BACKUS: NEUROSPORA FIG. 3

cluster of ascocarps—usually 5 to 12—matured. In the other instances no perithecia at all appeared. If two or three germinated conidia in a droplet of water were introduced, frequently as many small clusters of ascocarps were formed (Fig. 5, F–G), although the result varied with the size of the droplet which in turn determined the chance of appreciable separation of the spores.

In these tests extreme precaution was taken to avoid contamination, particularly through the introduction of microconidia, since with the technique employed this seemed the most likely error. Controls were rigidly maintained, and these showed in general that the amount of error from the source mentioned was negligible. It is hardly possible, however, to carry out hundreds of faultless conidiations of this type. That occasionally a mistake was made is certain. The distribution of perithecia in the lower left large circle in the plate culture illustrated in Figure 5, G, was in disagreement with expectations from the results of many other cultures. In the circle in question, two well-defined patches of ascocarps appeared, although according to the records only one conidium had been placed in that area. It may be assumed that in this case two conidia had accidentally been introduced. The writer is confident, however, that relatively few accidents of this kind occurred. Checks indicate an error of less than 2% due to failures in determining accurately the number of conidia applied, and one of less than 5% due to difficulties involved in the transfer of the conidia to the surface of the culture.

When single germinated ascospores derived from a cross between strains 56.6 and 56.4 were applied to marked areas on cultures of strain 56.6, over 60% of the spots remained sterile; but when perithecia developed, they were usually several in a small cluster.

Likewise, when a single ungerminated conidium was applied in a marked area just beyond the advancing margin of the mycelium (Fig. 5, C–G), several perithecia—with a maximum of about 20—typically appeared. The development of these perithecia was not uniform, some perithecia appearing several days after the first sclerotia had enlarged and darkened (Fig. 5, C–E). If more than one conidium was placed in the location described, as a rule proportionally more fruiting bodies appeared (Fig. 5). In a few cases in which observations were made, the conidia had begun to germinate at the time when the advancing hyphae of strain 56.6 were about to obliterate them from view.

To account for the observed development of a cluster of ascocarps following the application of a single germinating spore of the complementary strain to the sclerotia-studded surface of a culture, two hypotheses may be suggested. One is that of a localized "diploidization." An-

other possibility is that while spore germination is ordinarily inhibited by products of mycelial metabolism, these products do not entirely stop growth of germ tubes already put forth. Some direct evidence in favor of this latter idea has been presented in a preceding section of this paper. A dwarf mycelium might develop under such conditions from a conidium; and trichogynes from various sclerotial bodies as they were reached by this slowly advancing mycelium would probably obtain nuclei of the complementary strain by effecting union with ordinary vegetative hyphae. To the writer the latter hypothesis seems the more reasonable. It also seems probable that the development of several ascocarps obtained when a single ungerminated conidium is placed just beyond the margin of mycelial growth, is to be explained in similar fashion.

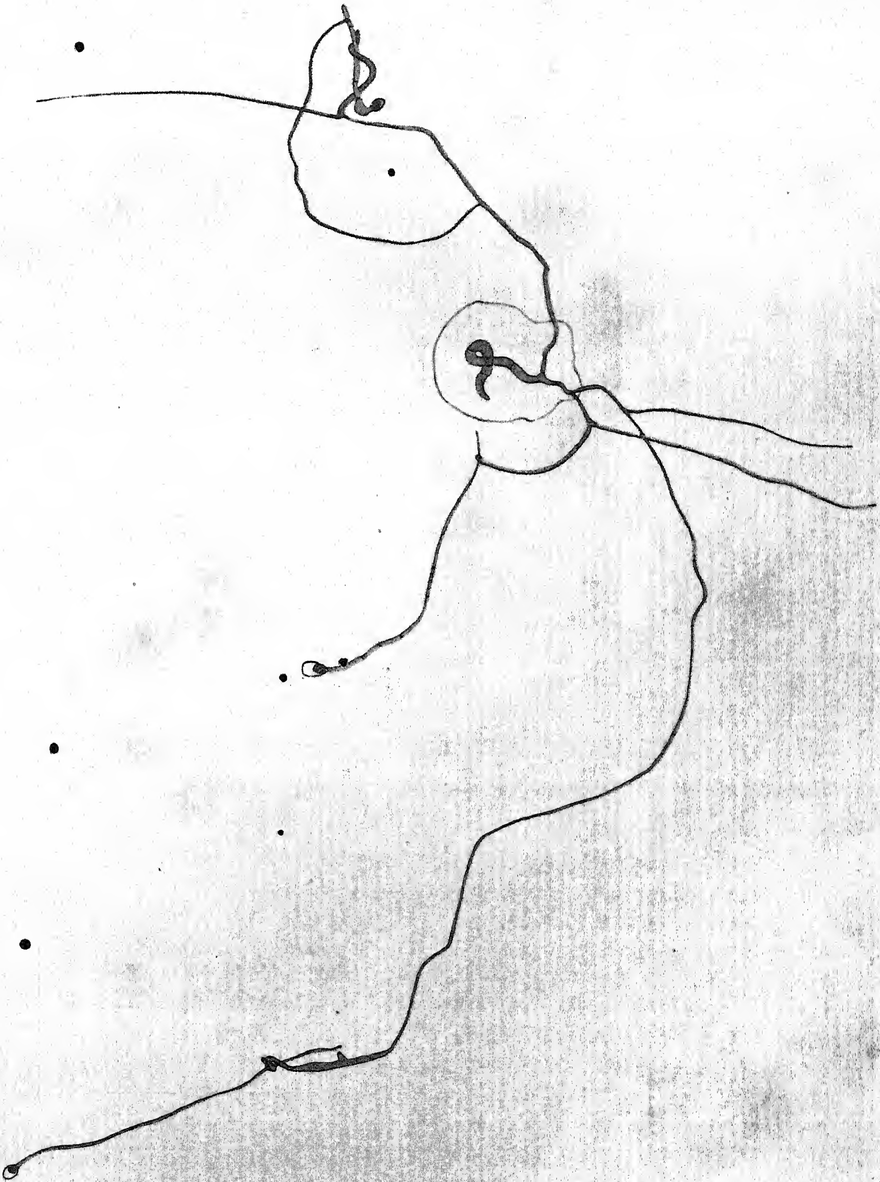
DISCUSSION

There has been given above an account of what happens when compatible conidia are placed in the vicinity of sclerotial bodies in cultures of *Neurospora sitophila*. It seems almost certain that when a detailed study of spermatial fertilization is undertaken, a picture very similar to what has been described in the case of conidial fertilization will be found. With the techniques employed in the present work a study of spermatial fertilization should present no great difficulties; and it seems very desirable that we should have the addition which such an investigation would contribute to our picture of the development of the perfect stage in this fungus. Despite the fact that in the case of a number of ascomycetes microconidia (spermatia) have now been shown to be functional bodies capable of effecting fertilization, no one has yet observed the actual fusion of these bodies with the trichogynes which have been shown to be present.

Experiments detailed in this paper have illustrated some of the various ways in which fertilization of sclerotial bodies of *N. sitophila* can be accomplished. That the transformation of sclerotial bodies into perithecia can be obtained by a variety of means was first shown by Dodge. In a paper published in 1935 (6) he refers to experiments—the details of which, however, are not given—which he says "indicate that young aerial hyphae and even trichogynes or trichogynous hyphae if they come in contact with trichogynous elements of the opposite sex reaction, are capable of effecting fertilization." It is evident that the thing of importance here is the introduction into the picture of cells of the complementary strain; and it is of

Explanation of Plate 4

Fig. 4. Relations of trichogyne system and germinated conidia, 9 hours after conidiation. ×175.



BACKUS: NEUROSPORA FIG. 4

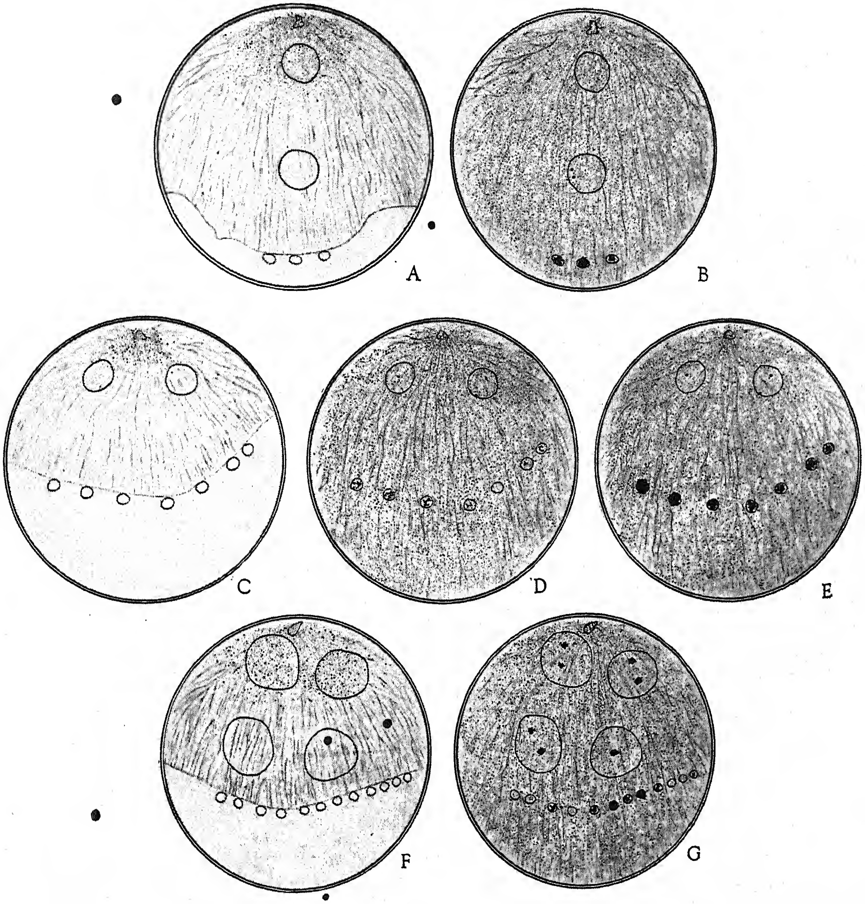


Fig. 5. A—Plate culture of *N. sitophila*, race 56.6 as it appeared at the time of conidiation (2 days after inoculation). Sclerotial bodies are abundant in upper large circle; no sclerotial bodies yet present in lower large circle. Ungerminated conidia of race 56.4 applied as follows: upper large circle—1 spore; lower large circle—9 spores; left small circle (just beyond margin of mycelium)—4 spores; center small circle—5 spores; right small circle—4 spores. B—The same plate 9 days after conidiation. 2 ascocarps in lower large circle; 20, 29, and 12 ascocarps in small circles, left to right. C—Plate culture of strain 56.6 at time of conidiation. Ungerminated conidia of strain 56.4 applied as follows: large circle at left—1 spore; large circle at right—3 spores; small circles, left to right, 6, 7, 5, 4, 4, 4, 1 respectively. D—The same plate 4 days later. E—The same plate 10 days later. F—Plate culture of strain 56.6 at time of conidiation. Sclerotial bodies abundant in the upper of the large circles, but absent in the lower two. To the large circles germinated conidia of race 56.4 applied as follows: upper left, 2 spores; upper right, 2 spores; lower left, 1 (?) spore; lower right, 1 spore. In the small circles just beyond the edge of the mycelium droplets from a suspension of ungerminated conidia applied. The droplets applied in succession to these circles, from left to right, were ascertained to be carrying spores as follows: no spores, no spores, 2 spores, no spores, 3 spores, 3 spores, 5 spores, 4 spores, 1 spore, no spores, no spores, 4 spores. G—Same plate 5 days later.

little importance in what form these cells are, provided their walls are not too thick (as in the case of ascospores). The present writer sees in this situation a remarkable case of plasticity and substitute sexuality—tendencies which are, however, by no means uncommon in ascomycetes. He is inclined to the view that the so-called microconidia are in reality male cells (spermatia) which, though still functional, are no longer essential to the development of the perfect stage. Dodge's (4, 5) observation that the microconidia of *Neurospora* may germinate supplies still further evidence of the plasticity of this fungus. If the conclusion is correct that the microconidia of *Neurospora* are male cells, then it follows that every race of *N. sitophila* may be considered hermaphroditic, since both male and female organs apparently may be formed on the same mycelium under suitable conditions. The performance of the sexual functions of the fungus appears to be regulated, however, by a superstructure of what may be termed compatibility factors which prevent self-fertilization. It is of course obvious that variability is favored by the compulsory interaction at every syngamy of two complementary strains.

N. tetrasperma Shear and Dodge (3, 11), a form with 4-spored asci, presents a peculiar situation in that one nucleus of each of the two compatibility groups is included in a single ascospore at the time of its formation. The mycelium which results when one of these ascospores germinates is essentially a mixo-chimaera. When ascogonia are formed they contain at the outset both kinds of nuclei; and ascocarps mature without the intervention of spermatia, conidia, or hyphae from any other mycelium. In fact it is reported (2) that no receptive hyphae are formed. Ordinarily, then, there is no occasion for spermatia to function in this form, or even scarcely any opportunity for them to do so. Yet these bodies are produced; and hence *N. tetrasperma* is hermaphroditic. Dodge (7) has designated this fungus as facultatively heterothallic since its ability to form perithecia on monosporous mycelia is due solely to the inclusion of two compatible nuclei in the same spore. Occasionally dwarf ascospores which contain only one nucleus at inception may be formed and these are not totipotent. They are either "A" or "B" in their reaction. An "A" thallus and a "B" thallus grown together in a petri dish react to produce perithecia. Dodge (5) has also shown that if monilioid conidia or spermatia from one strain are placed on marked areas of cultures of the opposite strain ascocarps will mature in these areas. It is thus clear that the spermatia of *N. tetrasperma* are not degenerate. One may suspect that the mechanism of fertilization in these cases where localized development of perithecia is obtained is probably the same as in *N. sitophila*. This seems all the more likely since Dodge (6) has found that the heterothallic races of *N. tetra-*

sperma form trichogynes. Dodge apparently did not study the situation in the normal races, but if Colson's conclusion that trichogynes are not formed in these is correct, it would seem, interestingly enough, that trichogynous outgrowths are produced in this species only when they can be of some service.

Gelasinospora tetrasperma Dowding is another facultatively heterothallic form, which is in many respects similar to *Neurospora tetrasperma* (10, 6, 8). In this species, however, neither spermatia nor conidia of any type have yet been discovered. It is possible that in the evolution of this fungus the spermatia, which became superfluous when the mixo-chimaera arrangement was developed, have completely disappeared from the picture. If so, all races of *G. tetrasperma* are essentially female; and when one mates heterothallic races, which may be obtained as in *Neurospora tetrasperma* (by germinating dwarf ascospores) and which fall into two compatibility groups, the bringing together of appropriate nuclei in the ascogonium is apparently accomplished through hyphal fusions and diploidization. Reduction seems to have proceeded further in *Gelasinospora* than in *Neurospora*, and neither the union of sexually differentiated protoplasts nor the range of substitute processes found in at least certain species of *Neurospora* is possible here.

SUMMARY

From a sclerotial body of *Neurospora sitophila* grows out a relatively complex branching trichogyne system originating from the apical region of the coiled ascogonium which lies in the interior of the sclerotial body. When a suspension of macroconidia of the complementary strain is placed on the surface of a culture bearing incipient perithecia, a union is effected between some of these conidia and various branches of the trichogyne system. The greater part of the protoplasm of the conidium enters the receptive trichogyne branch through a narrow cytoplasmic bridge.

Germinated conidia, germinated ascospores, and mats of mycelium of the proper strain also are capable of inducing the transformation of sclerotial bodies into perithecia. The details of the relations established between trichogynes and germinated conidia are described in the text.

Experiments are reported in which the number of ungerminated or germinated conidia applied to a given area was determined. On an average one perithecium is developed for every four or five ungerminated conidia placed on sclerotia-bearing regions of the culture. A single germinated conidium or ascospore similarly placed may, however, induce the development of a cluster of several ascocarps. A single ungerminated conidium placed just beyond the advancing margin of the mycelium frequently in-

duces likewise the development of a group of perithecia. A hypothesis is offered in explanation of these results.

The writer is grateful to Prof. E. M. Gilbert for counsel during the execution of this study. To Dr. B. O. Dodge and Prof. C. E. Allen he is indebted for helpful suggestions in the preparation of the manuscript.

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Additions to the Algae of Michigan*

Clarence E. Taft

(with twelve figures)

Previous to 1930 there had been no comprehensive survey of Michigan algae. A number of investigators had reported on isolated collections or localities, but none except Transeau (1917) had attempted to secure collections from widely separated areas. His work resulted in a list of 225 species, varieties, and forms, the largest single list published to that date.

Ackley (1932), following an extended survey of the state as well as a complete summary of the known literature on Michigan algae, published a list of 645 species, varieties, or forms of algae, exclusive of the Desmids and Diatoms, known to occur or reported as occurring in Michigan. During the same year (1932) Nichols and Ackley reported on the Michigan Desmids, listing 300 species, varieties, and forms for the state.

Since the appearance of these two papers in 1932 more than 100 additional records have been added by various workers.

The present list of 147 additional state records is the result of 155 collections made by the writer during the months of June, July, and August, 1936, while attending the summer session of the Michigan Biological Station, Douglas Lake, Michigan. Although a majority of the collections were made in the counties immediately surrounding the Station, some were secured in the Upper Peninsula, and a few in the western and southern parts of the state.

Of the 147 forms concerned in this report, there is one new species and one new variety, both in the genus *Oedogonium*. Of equal interest is the recording of several rare genera, a few of which have been figured.

With the exception of the county in which each species was collected, ecological data has been omitted.

To Dr. G. E. Nichols of the Department of Botany, Yale University, at whose suggestion the investigation was begun, I wish to express my sincerest appreciation for advice and aid during the collecting, and for certain determinations as acknowledged in the list of species, also to Dr. L. H. Tiffany of the Department of Botany, Northwestern University, and to Dr. E. N. Transeau of the Department of Botany, The Ohio State University, for criticism and advice concerning the Oedogoniaceae and the Zygnemales. For the correction of new records in the genus *Cosmarium* I am indebted to Dr. G. W. Prescott of the Department of Botany, Albion College. I am also indebted to the Michigan Biological Station for the

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use of collecting equipment, as well as to various staff members for information and transportation during the collecting.

The following are new species and varieties described in this paper:

Oedogonium minisporum Taft sp. nov.

Oedogonium oblongum Wittr. var. *minus* Taft var. nov.

SPECIES LIST

MYXOPHYCEAE

CHROOCOCCALES

APHANOCAPSA CASTAGNEI (De Bréb.) Rabenh. Cheboygan County.

EUCAPSIS ALPINA Clements and Shantz, Cheboygan, Presque Isle, Emmet and Otsego counties. This uncommon alga was found in a few of the bog lakes. The colonies were small and usually contained 8–32 cells.

GLOEOCAPSA RUPESTRIS Klebs, Otsego County.

GLOEOCHAETE WITTROCKIANA Lagerh. Cheboygan County. (Fig. 12). This interesting endophytic Myxophycean was found in two locations about three miles apart in Douglas Lake.

HOLOPEDIUM IRREGULARE Lagerh. Oakland County. (Figs. 10, 11).
Previously reported only from the plankton of a North Dakota lake. The colony is a rectangular, broadly corrugate plate, $80\mu \times 250\mu$. Cells irregularly arranged, 2–3μ in diameter.

MARSONIELLA ELEGANS Lemm. Emmet County. (Fig. 5).

RHABDODERMA LINEARE Schmidle and Lauterborn, Cheboygan County.

CHAMAESIPHONALES

PLEUROCAPSA MINOR Hansg. em. Geitler, Cheboygan County.

HORMOGONALES

ANABAENOPSIS ELENKINI V. V. Miller, Cheboygan County.

CALOTHRIX ADSCENDENS (Näg.) B. and F. Cheboygan County.
This alga was identified by Dr. G. E. Nichols from collections made by the class in Freshwater Algae, University of Michigan Biological Station, 1936.

PLECTONEMA WOLLEI Farlow, Cheboygan County. Also identified by Nichols.

SPIRULINA LAXISSIMA G. S. West, Cheboygan County.

HETEROKONTAE

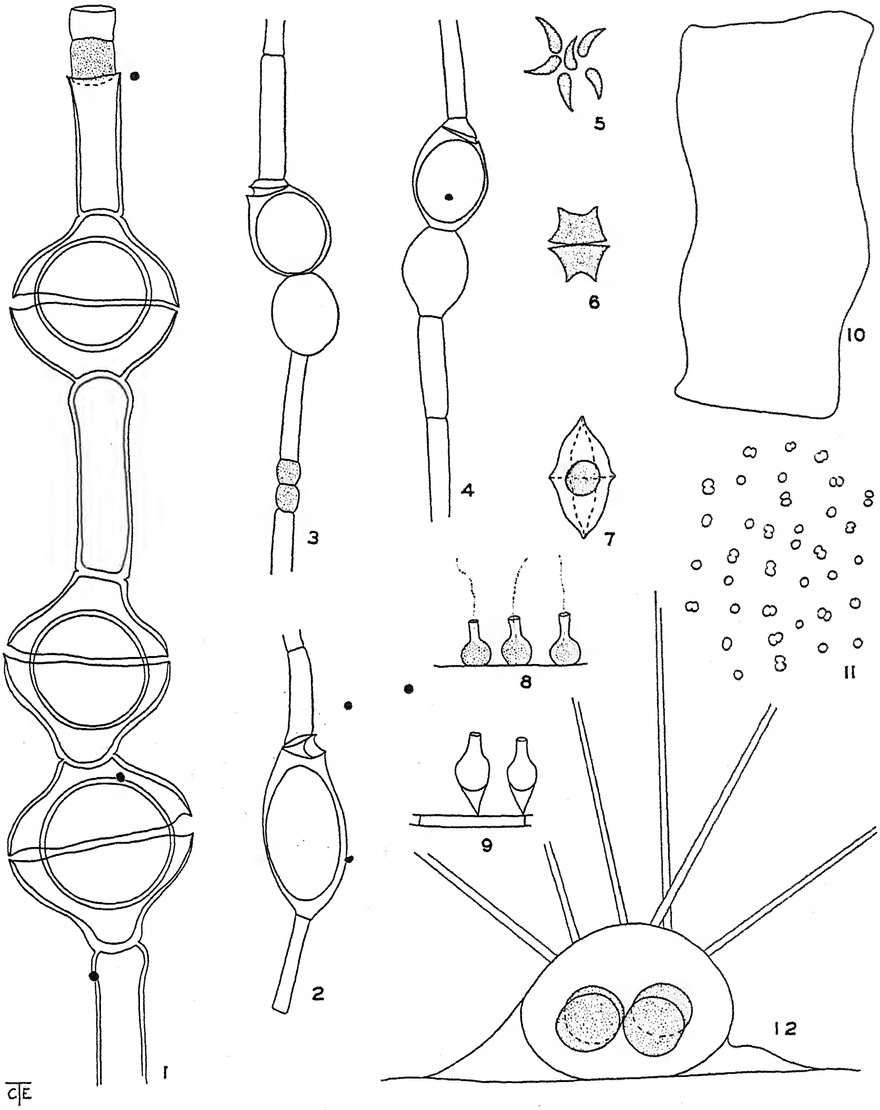
RHIZOCHLORIDALES

STIPITOCOCCUS URCEOLATUS W. & G. S. West, Grand Traverse County.

HETEROCOCCALES

CHARACIOPSIS LONGIPES (Rabenh.) Borzi, Macomb County.

OPHIOCYTIUM CAPITATUM var. LONGISPINUM (Mobius) Lemm. Cheboygan County.



Explanation of figures

Fig. 1. *Oedogonium minisporum* Taft sp. nov.
Figs. 2, 3, 4. *Oedogonium oblongum* Wittr. var. *minus* Taft var. nov.
Fig. 5. *Marsoniella elegans* Lemm.
Fig. 6. *Euastropsis richteri* (Schmidle) Lagerh.
Fig. 7. *Desmatractum bipyramidatum* (Chodat) Pascher.
Fig. 8. *Lagynion ampullaceum* (Stokes) Pascher.
Fig. 9. *Derepyxis dispar* (Stokes) Lemm.
Fig. 10. *Holopedium irregulare* Lagerh. Outline of colony.
Fig. 11. *Holopedium irregulare* Lagerh. Detail of cells.

CHRYSOPHYCEAE

Chrysomonadales

Derepyxis dispar (Stokes) Lemm. Macomb County. (Fig. 9).
Mallomonas caudata Iwanoff, Cheboygan County.

Rhizochrysidales

Lagynion ampullaceum (Stokes) Pascher, Cheboygan County. (Fig. 8).
Rhizochrysis limnetica G. M. Smith, Cheboygan County.

Chrysocapsales

Chrysocapsa planctonica (W. & G. S. West) Pascher, Cheboygan County.

CHLOROPHYCEAE

Volvocales

Gonium formosum Pascher, Cheboygan and Otsego counties.

Tetrasporales

Elakatothrix gelatinosa Wille, Cheboygan County.
Elakatothrix viridis (Snow) Printz, Cheboygan and Otsego counties.
Gloeocystis ampla Kuetz. Macomb, Cheboygan, Presque Isle, and Emmet counties.

Ulotrichales

Microthamnion kuetzingianum Näg. Cheboygan County.
Radiofilum conjunctivum Schmidle, Cheboygan County.
Uronema elongatum Hodgetts, Cheboygan County.

Oedogoniales

Bulbochaete angulosa Wittr. and Lundell, Cheboygan County.
Bulbochaete furberae Collins, Macomb County.
Bulbochaete nana Wittr. Cheboygan County.
Bulbochaete repanda Wittr. Cheboygan County.
Oedogonium exocostatum Tiffany, Cheboygan County.
Oedogonium minisporum Taft sp. nov. (Fig. 1).

Oe. monoicum, oogoniis singulis vel 2 continuis, subpyriform-globosis, raro subglobosis, operculo mediano apertis; oosporiis globosis, oogoniis non complentibus, membrana laevi; cellulis vegetativis capitellatis; antheridiis ?–2 sparis; cell. veget. 6–14$\mu \times$53–69μ; oogon. 30–42$\mu \times$34–42μ; oospor. 25–30$\mu \times$24–29μ; cell. antherid. 8–11$\mu \times$7–9μ.

Monecious; oogonia 1–2, subpyriform-globose, rarely subglobose, opening by a median operculum; oospore globose, rarely slightly subglobose, small, not filling the oogonium in either axis, color a pale yellow, wall smooth; vegetative cell capitellate; basal cell elongate; antheridia ?–2, sperms 2, division horizontal. Veg. cell 6–14$\mu \times$53–69μ; oogonium 30–42$\mu \times$34–42μ;

oospore 25–30$\mu\times$24–29μ; antheridium 8–11$\mu\times$7–9μ. Lake 16, Presque Isle County.

The combination of capitellate vegetative cells and small spores which do not fill the oogonium in either axis distinguishes this species from *Oed. psaegmatosporum* Nordst, which it superficially resembles in size and shape of the oogonium.

OEDOGONIUM MITRATUM Hirn, Macomb County.

Oedogonium oblongum Wittr. var. *minus* Taft var. nov. (Figs. 2, 3, 4).

Oogoniis singulis vel 3 continuis, oblongis, operculo apertis, circumscissone superiore vel supremo; oosporis ellipsoideis vel raro oboviformibus; cell. veg. 3–6$\mu\times$16–35μ; oogon. 13–16$\mu\times$20–23μ; oospor. 11–15$\mu\times$17–21μ; cell. antherid. 5–6$\mu\times$7μ. Oogonia 1–3, oblong, opening by a superior or sometimes supreme operculum; oospore ellipsoid, rarely obovoid, not quite filling the oogonium, color yellow-brown; suffultory cell sometimes enlarged. Veg. cell 3–6$\mu\times$16–35μ; oogonium 13–16$\mu\times$20–23μ; oospore 11–15$\mu\times$17–21μ; antheridium 5–6$\mu\times$7μ. Laizers Pond, Romeo. Macomb County.

This variety is separated from the species on the basis of size. In its dimensions it is approached by the variety *fusiforme* Jao, from which it differs in its smaller oogonia and oospores as well as the shape of the oogonium.

OEDOGONIUM AMBICEPS (Jao) Tiffany, Presque Isle County.

Veg. cell 9–12$\mu\times$30–40μ; oögonium 30–32$\mu\times$21–25μ; oospore 25$\mu\times$21μ; androsporangia 9–10$\mu\times$5–9μ.

Dimensions of the Michigan material have been given as they differ slightly from those given by Tiffany (1937).

OEDOGONIUM STELLATUM Wittr. Cheboygan County.

CHLOROCOCCALES

CHARACIUM ORNITHOCEPHALUM A. Braun, Cheboygan County.
CRUCIGENIA APICULATA (Lemm.) Schmidle, Otsego County.
CRUCIGENIA IRREGULARIS Wille, Otsego County.
CRUCIGENIA TETRAPEDIA (Kirchn.) W. & G. S. West, Cheboygan County.
CRUCIGENIA TRUNCATA G. M. Smith, Cheboygan County.
DESMATRACTUM BIPYRAMIDATUM (Chodat) Pascher, Macomb County. (Fig. 7).

This rare alga was collected in a sphagnum bog in which members of the class *Heterokontae* predominated.

Euastropsis richteri (Schmidle) Lagerh. Emmet County. (Fig. 6).

This alga, which has been previously reported from Wisconsin, was found in a small pool about three miles north of Pellston. The dimensions of the cells were well within the range given for this species, but as the figure shows, the apices of the cells are somewhat different, being broadly

retuse instead of notched. Smith, in his *Freshwater Algae of the United States*, says that it is possible to identify two-celled colonies of *Pediastrum* as *Euastropsis*. As *Pediastrum tetras* and *P. boryanum* were also in the collection, the writer hopes that further studies of Michigan algae will confirm this record.

FRANCEIA DROESCHERI (Lemm.) G. M. Smith, Emmet County.
GOLENKINIA RADIATA Chodat, Cheboygan County.
LAGERHEIMIA CILIATA (Lagerh.) Chodat, Cheboygan County.
LAGERHEIMIA CITRIFORMIS var. PAUCISPINA Tiffany and Ahlstrom, Cheboygan County.
PEDIASTRUM DUPLEX var. COHAERENS Bohlin, Macomb, Cheboygan, and Oceana counties.
PEDIASTRUM INTEGRUM forma GLABRA Raub. Emmet County.
QUADRIGULA CHODATI (Tanner-Fullman) G. M. Smith, Otsego County.
SELENASTRUM BIBRAIANUM Reinsch, Cheboygan County.
SCENEDESMUS ABUNDANS var. BREVICAUDA G. M. Smith, Emmet County.
SCENEDESMUS ACUTIFORMIS Schroeder, Macomb and Cheboygan counties.
SCENEDESMUS BRASILIENSIS Bohlin, Macomb and Otsego counties.
SCENEDESMUS PERFORATUS Lemm. Cheboygan County.
SCENEDESMUS QUADRICAUDA var. PARVUS G. M. Smith, Cheboygan County.
SCENEDESMUS QUADRICAUDA var. MAXIMUS W. & G. S. West, Cheboygan County.
SCENEDESMUS QUADRICAUDA var. WESTII G. M. Smith, Cheboygan County.
SCHROEDERIA JUDAYI G. M. Smith, Cheboygan County.
SORASTRUM AMERICANUM (Bohlin) Schmidle, Cheboygan and Otsego counties.
TETRAEDRON CAUDATUM (Corda) Hansg. Macomb, Presque Isle, Cheboygan, and Otsego counties.
TETRAEDRON CAUDATUM var. INCISUM Lagerh. Cheboygan County.
TETRAEDRON ENORME (Ralfs) Hansg. Cheboygan, Emmet, Otsego, and Manistee counties.
TETRAEDRON GIGAS var. GRANULATUM Boldt. Cheboygan County.
TETRAEDRON MINIMUM var. SCROBICULATA Lagerh. Cheboygan County.
TETRAEDRON TRIGONUM var. PAPILLIFERUM (Schroeder) Lemm. Cheboygan County.

ZYGNEMATALES

Zygnemataceae

MOUGEOTIA NUMMULOIDES (Hassall) DeToni, Emmet County.
MOUGEOTIA TENUIS (Cleve) Wittr. Cheboygan County.
SPIROGYRA ORIENTALIS W. & G. S. West, Cheboygan County.
ZYGNEMA CARINATUM Taft, Emmet County.
ZYGNEMA SYNADELPHUM Skuja, Cheboygan County.
ZYGNEMOPSIS MINUTUM Randhawa, Cheboygan and Emmet counties.

Mesotaeniaceae

CYLINDROCYSTIS BREBISSONII Menegh. Cheboygan County.
CYLINDROCYSTIS BREBISSONII var. MINOR W. & G. S. West, Presque Isle County.
GONATOZYGON BREBISSONII DeBary, Cheboygan County.
GONATOZYGON BREBISSONII var. MINUTUM W. & G. S. West, Cheboygan County.
GONATOZYGON KINAHANI (Arch.) Rabenh. Cheboygan County.
GONATOZYGON LEIODERMUM Turner, Cheboygan County.
GONATOZYGON PILOSUM Wolle, Cheboygan and Emmet counties.
MESOTAENIUM DE GREYI var. BREVE West, Cheboygan County.
NETRIUM DIGITUS var. LAMELLOSUM (DeBréb.) Grönblad, Cheboygan County.

Desmidiaceae

ARTHRODESMUS BULHEIMII var. SUBINCUS W. & G. S. West, Cheboygan County.
ARTHRODESMUS PHIMUS Turner, Cheboygan County.
ARTHRODESMUS PHIMUS var. OCCIDENTALIS W. & G. S. West, Cheboygan County.
ARTHRODESMUS TRIANGULARIS var. INFLATUS W. & G. S. West, Cheboygan County.
CLOSTERIUM ABRUPTUM West, Presque Isle County.
CLOSTERIUM ACICULARE var. SUBPRONUM W. & G. S. West, Presque Isle County.
COSMARIUM DECORATUM W. & G. S. West, Cheboygan County.
COSMARIUM DEPRESSUM var. RENIFORME W. & G. S. West, Cheboygan County.
COSMARIUM GLOBOSUM forma MINOR Boldt. Cheboygan County.
COSMARIUM HUMILE var. STRIATUM (Boldt.) Schmidle, Cheboygan County.
COSMARIUM ISTHMIUM West, Cheboygan County.
COSMARIUM NASUTUM Nordst. Cheboygan County.
COSMARIUM OBSOLETUM (Hantzsch) Reinsch, Cheboygan County.
COSMARIUM PSEUDOCONNATUM Nordst. Cheboygan County.
COSMARIUM QUADRUM Lund. Emmet County.
COSMARIUM REPANDUM forma MINOR W. & G. S. West, Cheboygan County.
COSMARIUM TINCTUM Ralfs. Cheboygan County.
DESMIDIUM COARCTATUM Nordst. Cheboygan County.
DESMIDIUM SWARTZII var. QUADRANGULATUM (Ralfs) Roy, Cheboygan and Presque Isle counties.
DOCIDIUM BACULUM DeBréb. Cheboygan County.
DOCIDIUM UNDULATUM Bailey, Cheboygan County.
EUASTRUM BINALE forma HIANS West, Cheboygan County.
EUASTRUM PECTINATUM var. BRACHYLOBUM Wittr. Cheboygan County.
EUASTRUM PULCHELLUM DeBréb. Cheboygan County.

Euastrum sinuosum var. reductum W. & G. S. West, Crawford County.
Euastrum ventricosum Lund. Cheboygan County.
Micrasterias apiculata var. fimbriata forma spinosa Bissett, Cheboygan County.
Micrasterias conferta var. hamata Wolle, Cheboygan County.
Micrasterias conferta var. novae-terrae Cushman, Cheboygan County.
Micrasterias expansa Bailey, Cheboygan County.
Micrasterias muricata (Bail.) Ralfs, Presque Isle County.
Micrasterias radiata var. gracillima G. M. Smith, Presque Isle County.
Micrasterias sol var. ornata Nordst. Cheboygan County.
Penium cucurbitinum forma minor W. & G. S. West, Cheboygan County.
Penium exiguum West, Cheboygan County.
Penium minutum (Ralfs) Cleve, Cheboygan and Presque Isle counties.
Sphaerozosma excavatum var. subquadratum W. & G. S. West, Cheboygan County.
Staurastrum contortum G. M. Smith, Cheboygan County.
Staurastrum curvatum W. West, Cheboygan County.
Staurastrum cuspidatum var. canadense G. M. Smith, Cheboygan County.
Staurastrum cuspidatum var. cornulatum Gutw. Cheboygan County.
Staurastrum longispinum (Bail.) Archer, Cheboygan County.
Staurastrum longispinum var. bidentatum (Wittr.) W. & G. S. West, Cheboygan County.
Staurastrum megacanthum var. scoticum W. & G. S. West, Cheboygan County.
Staurastrum ophiura Lund. Cheboygan and Otsego counties.
Staurastrum paradoxum var. longipes Nordst. Cheboygan County.
Staurastrum pentacerum (Wolle) G. M. Smith, Cheboygan County.
Staurastrum rotula Nordst. Cheboygan County.
Staurastrum sublaevispinum W. & G. S. West, Cheboygan County.
Tetmemorus brebissonii (Menegh.) Ralfs, Presque Isle County.
Tetmemorus granulatus (DeBréb.) Ralfs, Presque Isle, Crawford and Chippewa counties.
Tetmemorus granulatus var. attenuatus West, Cheboygan County.
Xanthidium armatum var. fissum Nordst. Cheboygan County.
Xanthidium armatum var. irregularius W. & G. S. West, Cheboygan County.
Xanthidium cristatum var. uncinatum DeBréb. Macomb, Cheboygan, Presque Isle, and Otsego counties.
Xanthidium torreyi Wolle, Cheboygan County.

DINOPHYCEAE

Gymnodinium palustre Schilling, Cheboygan County.

PERIDINIUM PUSILLUM (Penard) Lemm. Emmet County.
PERIDINIUM WILLEI Huitfeld-Kass, Cheboygan County.

EUGLENOPHYCEAE

PHACUS ACUMINATUS Stokes, Cheboygan County.
PHACUS PYRUM (Ehr.) Walton, Cheboygan and Otsego counties.
TRACHELOMONAS HISPIDA (Perty) Stein, Cheboygan and Emmet counties.
TRACHELOMONAS HISPIDA var. CORONATA Lemm. Oceana County.
TRACHELOMONAS HISPIDA var. PUNCTULATUM Skvortzow, Oceana County.
TRACHELOMONAS VOLVOCINA Ehrenb. Oceana County.

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The Cause of Pecky Cypress

WILLIAM A. MURRILL

(WITH SIX FIGURES)

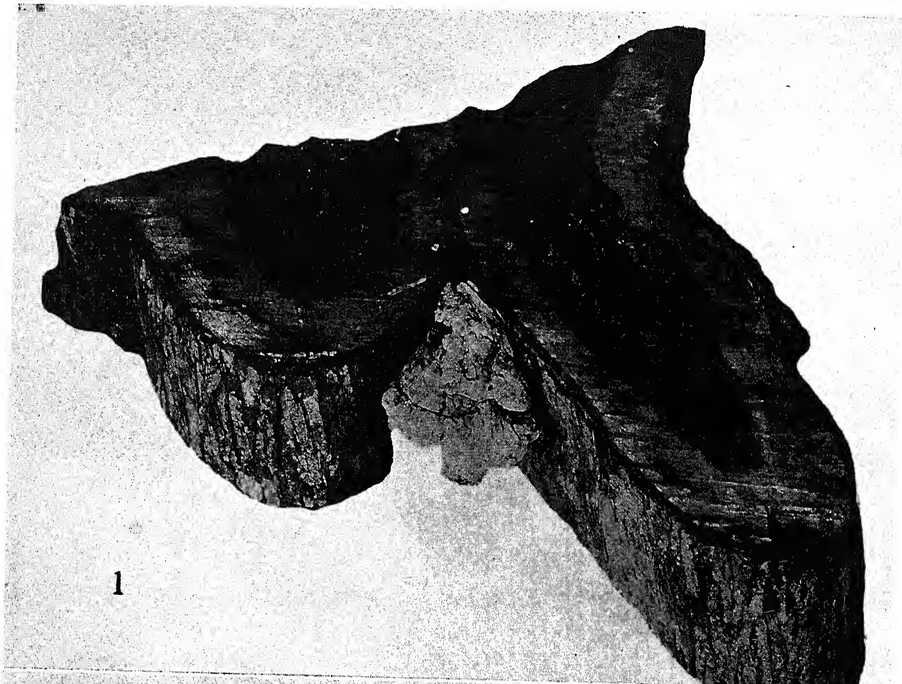
There was a time when "pecky cypress" lumber was thrown away or made to serve the lowliest purposes but now it shines in the halls of the mighty. For antiques and interior finishing it has few equals. It was even suggested to me recently that trees might have to be inoculated to meet the increasing demand. At present, only about ten per cent of our cypress trees show "peckiness."

The cause of "peckiness" is said to be the mycelium of a bracket fungus belonging to the genus *Fomes* in the Polyporaceae. It was first described by M. C. Cooke from British Guiana in 1884 (Grevillea **13**: 119) and was later found in other parts of tropical America and also in the southern United States. The name *Fomes geotropus* was selected for it because the dried brackets are noticeably curved downward. *F. Auberianus* (Mont.) Murrill, a species confined to tropical America, resembles it in form and habit but is much thinner and conspicuously zonate. *Fomes ulmarius* Fr., which attacks elms in Europe, is a still closer relative. The following scientific description of *F. geotropus* was used by the author in one of his publications:

Pileus woody, conchate, 6–12×10–20×2–4 cm.; surface pruinose to glabrous, rugose, anoderm, azonate, irregularly concentrically undulate, stramineous to cremeous; margin tumid, pallid, brownish when bruised, slightly undulate, deflexed; context corky to woody, pallid to isabelline, 0.5–1.5 cm. thick; tubes distinctly stratified, 0.5–1.5 cm. long each season, pale chestnut-colored, fading out in the older layers, mouths circular, 5 to a mm., edges thin, entire, rose-colored when fresh, becoming darker and discolored with age or when bruised; spores globose or subglobose, smooth, hyaline, granular, 5–7μ; cystidia none.

The Ellis Collection at the New York Botanical Garden contains a number of fine specimens of this fungus collected by Calkins and others on hardwood trunks in the Gulf States. Since coming to Florida I have collected it on box elder and magnolia, and the herbarium here also contains specimens found on sweet gum, linden, red bay, and winged elm. These were all taken from decayed trunks of living trees, usually near the base or in hollows, and infection doubtless occurred through wounds. About the middle of last August, Mr. West and I found some brackets on the side of an immense dead magnolia trunk which had been so weakened that it had blown over in a storm several years ago.

Johnson and Edgerton in their report upon *Fomes geotropus* on *Mag-*



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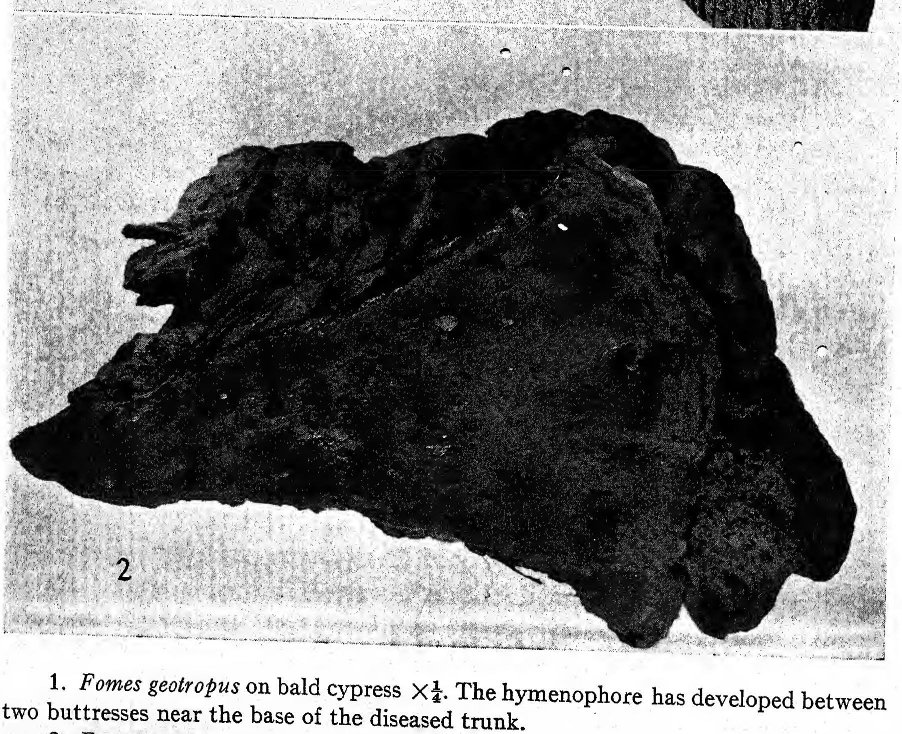
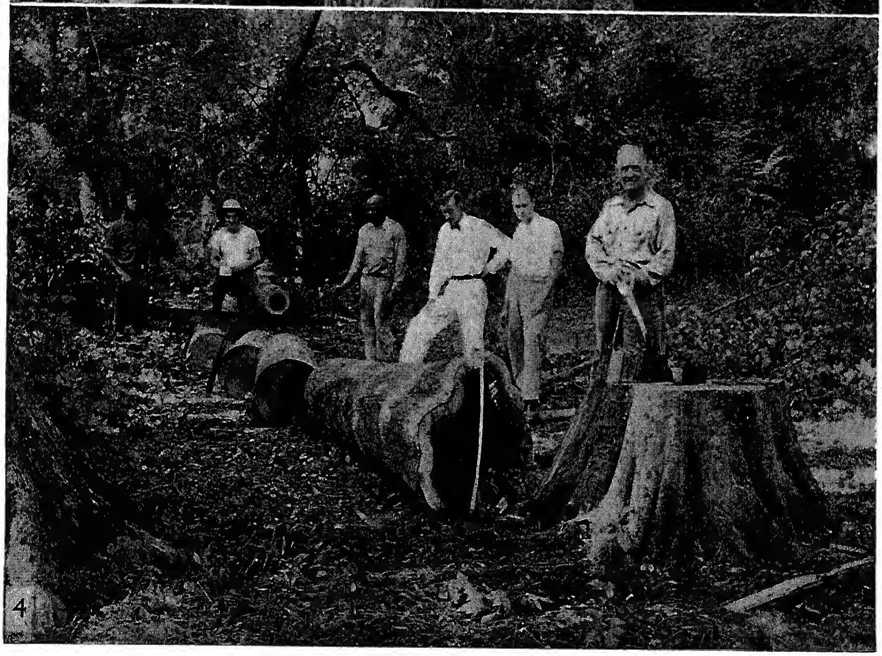


2

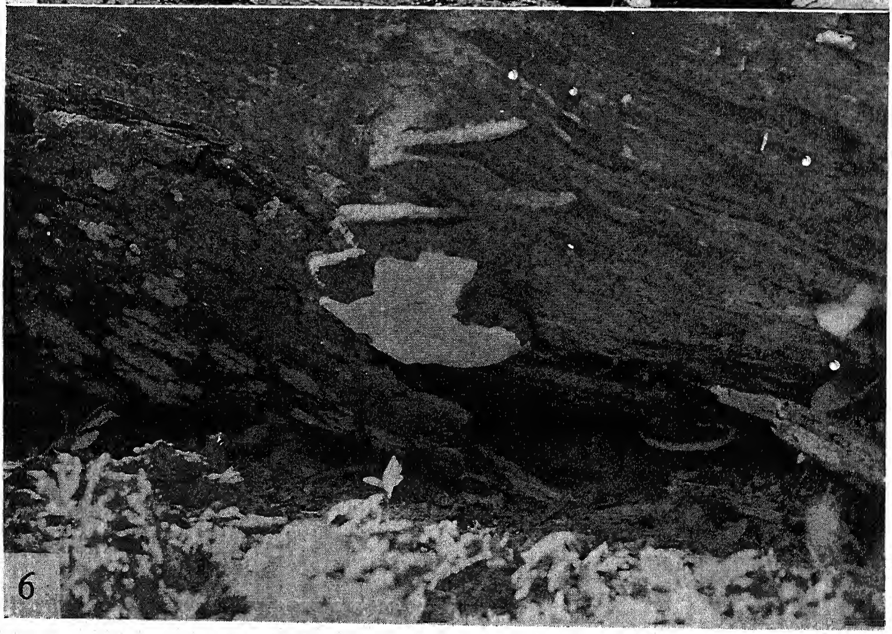
1. *Fomes geotropus* on bald cypress $\times\frac{1}{4}$. The hymenophore has developed between two buttresses near the base of the diseased trunk.

2. *Fomes geotropus* $\times 1$. This shows the under side of the hymenophore figured in Figure 1, which is six years old.



3. Stump of the tree hollowed out by the mycelium. In the foreground are the two buttresses between which the hymenophore appeared.

4. The cypress trunk cut into sections to trace the progress of the decay. The author is showing the position of the bracket, while next beyond him are Messrs.



5. Termination of the decay shown at the center of two adjacent sections of the trunk.

6. *Fomes geotropus* on a dead magnolia log. The mass is about a foot high and six inches wide, the upper surface old and discolored, the hymenium fresh and cream-colored. Photo by Dr. R. P. Wodehouse.

nolia grandiflora in Louisiana (Mycologia **28**: 293. 1936) make no mention of finding the brackets on the dead fallen logs but only near the base of diseased living trunks. Mr. W. H. Long (Phytopathology **4**: 39. 1914) states that he found the hymenophores on magnolia and also upon tupelo gum, black gum, sweet gum, elm, and maple among the hardwoods, as well as upon bald cypress.

The occurrence of the brackets upon cypress trunks seems to be rare, otherwise they would have been more frequently found. On July 27, 1938, Mr. West and I were exploring a hammock south of Newnan's Lake, a few miles from Gainesville, when we stumbled upon a tree of *Taxodium distichum* bearing a bracket of what appeared to be *Fomes geotropus* upon its trunk three feet above the ground. It had grown out between two buttresses and proved to be six years old. Mr. Adolph Vidal, the owner of the land, kindly gave us permission to cut the tree, which we did on August 25, 1938.

Assisting us in the investigation of the rot in this particular tree were Dr. G. F. Weber, Plant Pathologist in the Florida Agricultural Experiment Station, Mr. R. K. Voorhees, Assistant Plant Pathologist, and Dr. A. S. Rhoads, Plant Pathologist at Cocoa, Florida. The photographs were taken by Dr. Weber and all the records were made by Mr. Erdman West, Mycologist in the Florida Agricultural Experiment Station.

As the illustrations will show, sections were made of the trunk at various points and the decay traced from the hollow base upward along the trunk to its termination in sound wood. The fungus probably entered the trunk at a wound or burn near its base, and, after years of growth, the bracket probably emerged at or near the same point. When infection takes place at a broken branch some distance above ground, the mycelium probably travels both upward and downward in the trunk and brackets are formed wherever there are openings to the light. If the branch stub does not heal over, this would be a very likely place to look for a bracket.

In a pamphlet recently sent me by the Southern Cypress Manufacturers Association, with offices at Jacksonville, the following description of the decay in bald cypress is given:

"The fungus invades the trunk of the tree, which it honey-combs in varying degrees, leaving pockets in the wood from a quarter of an inch to an inch in diameter and often several inches long. These pockets are filled with a brown powder, a deposit from the fungus, antiseptic in action, which in time apparently arrests the further progress of the fungus itself. Another peculiarity of this fungus is that it stops working as soon as the tree is felled and never again attacks wood sawn from these infected trees."

The appearance and effects of this rot in cypress have long been known.

The self-toxicity of the mycelium, however, might be open to discussion; and why the fungus ceases to grow in cypress when it is cut and develops brackets on a magnolia log years after the trunk is dead is another question not so easily answered. It may be that careful cultures and inoculations will help to solve these questions as well as certain other puzzles connected with this very interesting fungus. But, as the young doctor said to himself while scattering bottles on a lonely curve, in this business one must have patience.

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Barbula in North America north of Mexico[1]

William Campbell Steere

Hedwig, in his classic "Species Muscorum" (1801), described as new five species of *Barbula*, *B. acuminata*, *B. agraria*, *B. apiculata*, *B. lanceolata*, and *B. stricta*, from American specimens. Since the appearance of Hedwig's publication, more than sixty other species of *Barbula* have been described as new or reported to occur in North America north of Mexico, not counting the twenty-odd species of *Barbula* which are really members of the genus *Tortula*.

Most of the species were described by various European bryologists, of necessity unfamiliar with the great range of variation of each species in the field. The original descriptions appeared in a multitude of scientific journals, reports of expeditions and other publications, many of them abroad. As a result of the scattering of descriptions and specimens for comparison, it apparently became progressively easier for authors to describe more new species than to identify the old ones.

Perhaps, also, a false diagnostic value was placed upon extremely variable characteristics in an extremely variable group of species. Nearly every diagnostic character used in *Barbula* varies within rather wide limits and most species are best identified by a complex of characteristics rather than by any single one. This situation is especially well discussed by Hilpert (1933) whose interesting researches demonstrate the very slight amount of taxonomic significance to be derived from such characteristics as, for example, the presence of a central strand in the stem, the shape of the stem in cross section, and the size of the annulus. This last structure, given a good deal of taxonomic importance by earlier bryologists, is shown to be completely valueless as a diagnostic feature by Hilpert, the only valid distinction being between the persistent and the revoluble annulus.

The choice of single, very variable characteristics to separate species, by earlier authors, often lead to their confusion. For instance, Lesquereux (1865) maintained *Barbula flexifolia* Hampe as a valid species, comparing it to *B. vinealis* Brid., as follows: "The characters separating this species from *Barbula vinealis* are, 1st, The leaves crisped when dry, squarrose-reflexed when humected, with revolute margins. 2d, The somewhat narrower, dark red capsule, with a longer operculum. 3d, The longer and more twisted teeth of the peristome, and their red color. These last characters are unreliable, the teeth varying in color, and being more or less twisted even on the same specimen, according to the age of the capsule. The char-

[1] Papers from the Department of Botany and the Herbarium of the University of Michigan, No. 674.

acters taken from the leaves are also unreliable." The differences between *B. cylindrica* (Tayl.) Schimp. and *B. vinealis* Brid. are still puzzling, of course, but we may now use a large series or complex of quantitative criteria and thus separate two closely related species on a more or less statistical basis.

One usage of the earlier authors seems to me clearly to violate an important biological principle. In general, little evidence supports the expectation that several closely related species of the same genus can maintain themselves as separate and independent species if they occupy exactly the same habitats and geographic ranges. In fact, each species seems to occupy a small niche in the environment in which it does not compete to any extent with other species in the same genus, certainly not those which are closely related. If two species have exactly the same habitat, ordinarily they have different geographic ranges, or are not at all close phylogenetically. Consequently, when an author manages to identify three or four species of the same genus, of which perhaps one is proposed as a new species, from the very same tuft, there seems good reason to suspect that he is confusing habitat or genetic variability with his species concept.

No real effort has ever been made to clear away the confusion which surrounds almost every one of our American species of *Barbula*, probably because of the labor involved and also because of the large number of genera which are in exactly the same condition, for the same reasons. The only survey of the American species of the genus *Barbula* is that in Lesquereux and James' "Manual," published in 1884. Insofar as *Barbula* is concerned, at least, the treatment was essentially a compilation. Although a few comments were made concerning the presumptive identity of two or more "species," no critical attempt was made to settle definitely any of these problems. In the more than a half-century since the "Manual" appeared, critical notes on a few species have been published and several conscientious bryologists have indicated their opinions as to probable synonymy in herbarium notes. It is more than likely that the large number of new species proposed by N. C. Kindberg, alone or in collaboration with C. Müller, has been responsible in large part for the delay in any attempt to revise the American species of *Barbula*.

During the past two years, which have been spent in the revision of the genus *Barbula* for Dr. A. J. Grout's "Moss Flora of North America, north of Mexico" (Steere, 1938b), I have had occasion to see the type material of nearly every one of the species of *Barbula* originally described from our range, thanks to the kindness of many individuals and institutions. It has been found possible to reduce the great assemblage of species of *Barbula* to a tentative order, and to identify the majority of the species more

recently proposed as new with older and better established species.

Since many of the reductions of names to synonymy and recommendations for the summary discard of others are perhaps open to criticism, I am taking this opportunity to present my reasons for the disposition of each name. As such a series of critical notes, especially when its bearing is largely upon nomenclature and taxonomic status, is of no particular importance in identification, and so is beyond the scope of a manual, most of the comments which follow serve to supplement but not duplicate those which have already appeared in the revision of *Barbula*. It is hoped that the disposition of many specific names which have not appeared in the literature for several decades, but which still exist as puzzles in every herbarium, may be of some use to those beset by such puzzles.

In the following list of species, I have almost completely ignored the new varieties which Kindberg proposed because quite uniformly they do not even belong to the species to which he assigned them. Also nearly every variety has a very involved history, as for example his "*Barbula gracilis* var. *squarrulosa*" which he later cited as a synonym of his new species "*Barbula subicmadophila*," which in turn is actually a synonym of *B. rubiginosa* Mitt., with no relationship whatsoever to either *B. gracilis* or *B. icmadophila!* After a few experiences of this sort, I did not go to the trouble of identifying the remainder of Kindberg's "new" varieties, and should recommend that they be totally disregarded, at least in *Barbula*.

The following species of *Barbula*, which have been described as new from specimens collected in our range, no longer fit our concept of the genus *Barbula*, as a result of the drawing of narrower generic lines, and for the most part belong to *Tortula: B. astoriensis* Broth., *B. Bolanderi* Lesq., *B. brachyangia* C. Müll. & Kindb., *B. brachypoda* Card. & Thér., *B. brevipes* Lesq., *B. carnifolia* C. Müll. & Kindb., *B. Egelingi* Schlieph., *B. laeviuscula* Kindb., *B. latoexcisa* C. Müll. & Kindb., *B. leptotricha* C. Müll. & Kindb., *B. macrotricha* Card. & Thér., *B. megalocarpa* Kindb., *B. papillinervis* C. Müll. & Kindb., *B. pseudoaciphylla* Kindb., *B. rotundo-emarginata* C. Müll. & Kindb., *B. rufipila* Card. & Thér., *B. subcarnifolia* C. Müll. & Kindb., *B. subcuneifolia* Kindb., *B. submegalocarpa* Kindb.

Species of Barbula Described or Reported from North America[2]

1. *Barbula acuminata* Hedw., Sp. Musc. **117.** 1801.

Hedwig himself appended to his diagnosis of the species the remark "An haec eadem, quae mea barbula *unguiculata?*" and Schwaegrichen

[2] Valid names are written in capital letters, those reduced to synonymy in italics.

later affirmed this query. Cardot (1899), however, as the result of his study of the type material and Hedwig's illustrations, considered it a synonym of *B. fallax* Hedw., and is followed by Paris (1904). This name, based on a specimen from Lancaster, Pennsylvania, was either neglected and forgotten, or else misused, yet occasional specimens bearing it are still encountered. Although I have not seen the type specimen, I am convinced, from Cardot's words, that it is *B. fallax.*

2. BARBULA ACTUA (Brid.) Brid., Method. Musc. **96.** 1822.
Tortula acuta Brid., Musc. Recent. Suppl. **1:** 265. 1806.
Barbula gracilis Schwaegr., Sp. Musc. Suppl. $\mathbf{1}^1$**:** 125. 1811.

This species, which seems usually to pass under the name of *B. gracilis* in the American literature, has been reported from a number of widely separated localities. Its greatest abundance or most general occurrence seems to be in British Columbia, Idaho, Montana, New Mexico, Arizona and California, yet there are a few specimens from scattered stations in the eastern United States, from New England southward, in the mountains. The specimens are all rather perplexing, however, for very few of them agree really well with European material, all being slightly papillose and differing in other more subtle and indefinable ways. What adds still more difficulty to the problem of identifying the so-called American *B. acuta* is that the eastern and western specimens do not agree well. This fact, in view of the great variability of the material, which apparently fruits only very rarely, and the very curious geographical distribution of the supposed species in our range, arouses the suspicion that we may be dealing here with a complex of two species, one or both of which may be different from the European *B. acuta.*

3. BARBULA AGRARIA Hedw., Sp. Musc. **116.** 1801.
Tortula agraria Sw., Fl. Ind. Occ. **3:** 1763. 1806.
Barbula Raui Aust., Bull. Torrey Bot. Club **6:** 43. 1875.

This species, which was described from Jamaica and Santo Domingo, and is widespread through tropical and subtropical America, has been placed about equally often in *Barbula* and *Tortula* by various authors. In the structure of the costa, in cross-section, the relationship is evidently to *Barbula.* The shape of the leaf, on the contrary, is typically that of *Tortula*, in which the leaf becomes wider above a narrow base. The leaf margins are plane when moist and somewhat involute when dry, neither condition characteristic of *Barbula.* The peristome, however, is aberrant for either genus, and there are perhaps sufficient differences otherwise to justify eventually the erection of a new genus. For *B. agraria* and related species, Müller (1849) erected the section *Hyophiladelphus.* Brotherus

(1924) recognized this section, but restricted it to include only *B. agraria* and several too closely related species. Those from the West Indies and Central America will eventually turn out to be conspecific, no doubt.

4. *Barbula amplexa* Lesq., Trans Amer. Phil. Soc. **13:** 5. 1865.

The original description of this species very clearly indicates the genus *Tortula*, and Lesquereux compared it somewhat indirectly to *T. marginata* (Bry. eur.) Spruce. In spite of this authoritative evidence that the species should be transferred to *Tortula*, it has been widely distributed in relatively recent exsiccati as *B. amplexa*, *No. 180* in Holzinger's "Musci Acrocarpi Boreali-Americani," for example. Furthermore, Brotherus, in the second edition of Engler und Prantl (1924, p. 280) retained it in *Barbula*, and, on the basis of the sheathing perichaetial leaves, placed it in the section *Streblotrichum*. I have examined the type material, however, and can substantiate, without question, Lesquereux's implication that the species is a member of the genus *Tortula*, although it cannot be safely said yet whether or not it is a valid species in *Tortula*.

5. *Barbula andreaeoides* Kindb., Rev. Bryol. **32:** 36. 1905.

This remarkable little moss with obtuse, cochleariform leaves is obviously no *Barbula* at all, but a form of *Andreaea Rothii* Web. & Mohr. I am grateful to Dr. A. J. Sharp for confirming my disposition of this "species."

6. *Barbula apiculata* Hedw., Sp. Musc. **117.** 1801.

This species is based on a specimen which came, insofar as the original description informs us, from "Pensilvania." According to Cardot (1899), the type specimen, which he has examined, bears on its label the notation that it was collected at Lancaster. He also concluded that the type material represents the form of *B. unguiculata* Hedw. called var. *apiculata* in the Bryologia Europaea.

7. *Barbula artocarpa* Lesq., Trans. Amer. Phil. Soc. **13:** 4. 1865.

Lesquereux says of this: "Except for its pretty large annulus, this species would agree with *Barbula gracilis* Schw., which it exactly resembles by the ramification, the form of the leaves and of the capsule." I have seen the type specimens, from Mount del Diablo, California, and find that the leaf cells are rather distinctly papillose, and that several characteristics preclude any relationship to *B. acuta*. In fact, from the widely spreading leaves, the strongly recurved leaf margins, the costa ending in the leaf apex and the pale, dusty red peristome, the only possible conclusion is that *B. artocarpa* is only a small form of *B. vinealis* Brid., and must become a synonym of it.

8. *Barbula Bakeri* Card. & Thér., Bot. Gaz. **37**: 367. 1904.

The problem as to the use or disposal of this name is very difficult to settle satisfactorily. Several different collections, each from a different station, were issued as "*Barbula Bakeri* Card. & Thér. n. sp." Furthermore, all these not too similar specimens are cited in the original description, with no indication as to which one should be considered the type. The problem is made still more perplexing by the fact that at least two different species are represented in the collections. In a comment supplementary to the original description, and published also on the label of both Baker's "Pacific Slope Bryophytes" *No. 33*, and Holzinger's "Musci Acrocarpi Boreali-Americani" *No. 157* (=Baker's "Pacific Slope Bryophytes" *No. 351*), the authors say: "A species belonging to the perplexing group of B. fallax Hedw., differing from this species by its smooth or very slightly papillose leaves with margins more broadly revolute, and by its shorter, slightly twisted peristome."

As shown elsewhere, *B. fallax* Hedw. is out of the question anyhow, since it apparently does not occur west of the Rocky Mountains. All the specimens issued as *B. Bakeri* have short cells on the ventral surface of the costa, which still further eliminates any possibility of a relationship to *B. fallax*. The original description suggests a member of the *B. vinealis* group, which is substantiated by an examination of the original material. Baker's *No. 33*, mentioned above, collected at "Stanford University, Santa Clara County, California, October 26, 1901; common in small mats on stones bordering flower beds" is fairly typical *B. vinealis*. Baker's "Pacific Slope Bryophytes" *No. 352*, from "Foothills near Stanford University, Santa Clara County, California, March 22, 1902" is a smaller plant with a much shorter seta. Baker's *No. 351*, collected at "Alma, Santa Clara County, California, March 23, 1902; on a boulder" was issued, still with Baker's label, by Holzinger as *No. 157* in his "Musci Acrocarpi Boreali-Americani" with the comment: "Type station, Stanford University." Baker's *351* and *352* are rather similar, but differ from *B. vinealis* in the more uniform areolation and the leaves being rather strongly revolute from base nearly to apex. From these characteristics, as well as the short, only slightly twisted peristome, a form of *B. brachyphylla* Sulliv. with rather more acute leaves than usual, seems to be indicated.

9. *Barbula Beecheyi* Lesq. in Watson, Bot. Calif. **2**: 372. 1880.

According to Lesquereux and James (1884) this is a synonym of *B. cylindrica* (Tayl.) Schimp.

10. Barbula Bescherellei Sauerb. in Jaeg., Adumb. **2**: 673. 1878. *B. rigidula* Besch., Prodr. Bryol. Mex. **36**. 1871, not *B. rigidula* (Hedw.) Milde.

Mr. Bartram has recognized this Mexican species in our range, from both Arizona and New Mexico. Concerning its distribution in Arizona, he says (1927): "It is abundant in the oak forests of the Patagonia and Santa Rita Mts., and frequently grows in dense cushions around the bases of the trees. The species is ordinarily sterile in Arizona but a fertile colony of several hundred plants was found on shaded ledges along the Baldy Trail, Santa Rita Mts., at an elevation of about 6500 feet."

The species differs from *B. acuta* (Brid.) Brid. in the generally larger size of the whole plants, longer stems and leaves, more revolute leaf margins, much longer capsules, and the longer, more twisted peristome teeth.

11. BARBULA BRACHYPHYLLA Sulliv., Rept. Pacific R. R. Surv. (35th Parallel) **4**: 186. 1856.

The typical form of this specis is very clear cut and distinct in its short leaves which may reach 1.5 mm. The leaves are also characterized by the very uniform areolation, the margins revolute from base to apex, and the sometimes obtuse apex. Furthermore, the peristome teeth are short and only slightly twisted. The short cells composing the ventral surface of the costa, and the dusty red peristome which becomes paler with age clearly ally this species with the *B. vinealis* complex. Many forms exist which are not altogether typical and which point to a still closer relationship to *B. vinealis*. Some of the material issued as *B. Bakeri* Card. & Thér. (q. v.) is clearly to be placed here in spite of the acute leaves, which may even end in a single pellucid cell exactly as in many forms of *B. vinealis*. *B. purpurea* C. Müll. is also most appropriately admitted to synonymy here. In the last analysis, then, we may consider *B. brachyphylla* simply as the most reduced form of the extremely variable *B. vinealis*-*B. cylindrica* complex.

12. *Barbula chrysopoda* C. Müll. & Kindb. in Macoun, Cat. Canad. Pl. **6**: 57. 1892.

The original material upon which this species was based is absolutely typical *B. convoluta* Hedw. I have examined all the material named *B. chrysopoda* by Kindberg, from the National Museum in Stockholm and from the Canadian National Herbarium in Ottawa, and can find not even one characteristic by which this may be separated from *B. convoluta*. It is true that western forms of *B. convoluta* are apt to have larger perichaetial leaves with a better developed costa, but the difference is so subtle and so completely bridged by intermediate forms that there is no justification even for a form. The very long operculum attributed to *B. chrysopoda* (Kindberg, 1897) is just as characteristic of *B. convoluta* Hedw.

13. *Barbula circinnatula* C. Müll. & Kindb. in Macoun, Cat. Canad. Pl. **6**: 56. 1892.

The original specimens, from Agassiz, British Columbia, upon which this name was based are fairly typical *B. cylindrica* (Tayl.) Schimp. The upper leaves on the stem are much longer, up to 5.0 mm. long, and conspicuously contorted and crisped when dry, and in other ways there is good agreement with *B. cylindrica.*

14. *Barbula cancellata* C. Müll., Flora **56**: 483. 1873.

I have seen type material of this species (from Texas) and can unhesitatingly pronounce it to be typical *B. Cruegeri* Sond. Even the multicellular axillary propagula are present on the type specimens. The remarkable peristome, in which the teeth are often cancellate or trabeculate at the base and appendiculate above, has led to the transfer of this species to *Dialytrichia* by Kindberg (1897), where it has been maintained by Brotherus (1909, 1924). *B. cancellata* has no relationship to *Dialytrichia,* however, especially in any gametophytic characteristics, but as already indicated, is really *B. Cruegeri,* which is more closely related to *B. unguiculata* Hedw. An interesting confirmation of this fact is that several specimens of *B. unguiculata* specially examined were found to have somewhat cancellate peristomes. The typically cancellate peristome of *B. Cruegeri* is exceedingly well demonstrated by Renauld and Cardot's "Musci Americae Septentrionalis Exsiccati" *No. 23.*

15. *Barbula Closteri* Aust., Bot. Gaz. **1**: 29. 1876.

The New Jersey specimens from which Austin described this species are very perplexing, as they are extremely depauperate and fragmentary. They approach *B. Cruegeri* closely enough, however, to allow us to unite the two species with reasonable safety. Several circumstances tend to substantiate this view. The Florida specimens of *B. Closteri* cited by Austin, although sterile, are definitely only poorly developed specimens of *B. Cruegeri.* Furthermore, a number of species thought to be restricted to the southern Coastal Plain have been discovered in New Jersey and on Long Island. Perhaps the best examples of this type of distribution are the recent discoveries of *Syrrhopodon texanus* Sull. (Cain, 1936; Grout, 1937) and *Syrrhopodon floridanus* Sull. (Wickes, 1937), on Long Island, New York.

Austin, in the original description of *B. Closteri,* suggested that it is "nearest to *B. convoluta*" in spite of the fact that some of his specimens bear archegonia, yet have absolutely no development of convolute-sheathing perichaetial leaves. Austin's misconception has been accepted and

brought into modern literature by Brotherus (1924) who includes it under the section *Streblotrichum*.

16. Barbula convoluta Hedw., Sp. Musc. **120.** 1801.
B. chrysopoda C. Müll. & Kindb. in Macoun, Cat. Canad. Pl. **6:** 57. 1892.

This species is so common, widespread, and easily recognized that very little comment is necessary. In general, the American plants have shorter, fewer, and consequently less conspicuous perichaetial leaves than European specimens. However, the perichaetial leaves of American specimens tend to be more strongly costate.

17. Barbula Cruegeri Sond. in C. Müll., Syn. Musc. **1:** 618. 1849.
Tortula Cruegeri Mitt., Musc. Austr. Amer. **150.** 1869.
Barbula cancellata C. Müll., Flora **56:** 483. 1873.
B. Jooriana C. Müll., Bull. Torrey Club **5**(12): 49. 1874.
B. Closteri Aust., Bot. Gaz. **1:** 29. 1876.
B. Ravenelii Aust., Bot. Gaz. **2:** 89. 1877.
Tortula Closteri Aust., Bot. Gaz. **3:** 30. 1878.
Dialytrichia cancellata Kindb., Eur. & N.-Amer. Bryin. **291.** 1897.
Desmatodon Bushii Card. & Thér., Bot. Gaz. **37:** 366. 1904.

In spite of its frequency and wide distribution in the southern Coastal Plain, this species has remained seriously misunderstood, a statement vouched for by the extensive synonymy. It has a very superficial resemblance to the related *B. unguiculata* Hedw., which has resulted in a confusion of the two species by many competent workers, although they are really very distinct and there is even practically no overlapping in their geographical ranges. The smaller size, paler color, and red stems are characteristics which serve to distinguish *B. Cruegeri* in a sterile condition. The one absolutely unmistakable characteristic, yet one whose diagnostic value has not previously received recognition, is the presence of numbers of reddish, multicellular, axillary propagula, which will be found on the great majority of plants. On some specimens careful search is necessary to demonstrate the propagula, but on others the propagula are so numerous that the whole plant is given a reddish tinge. The sporophyte is characterized by its smaller size throughout; the capsule is shorter, paler and thinner walled than in *B. unguiculata*. The peristome is fugaceous and often strongly cancellate at the base. (See remarks under *B. cancellata* C. Müll.)

There is still some doubt in my mind as to the use of the name *B. Cruegeri*. Our plant, in its typical propaguliferous form, occurs throughout the hot tropical lowlands, especially in the West Indies. However, what is apparently another species, without propagula, from the high mountains

of Central and South America, is also called *B. Cruegeri.* I have not yet been able to see the type specimen of the species, from Trinidad, but rely for my use of the name on the words of Renauld and Cardot (1896), in reference to their "Musci Americae Septentrionalis Exsiccati," *No. 23:* "Ces échantillons de la Louisiane sont complètement identiques à ceux provenant de l'île de la Trinité, de l'Equateur et du Pérou." If, however, the type material of *B. Cruegeri* turns out to represent the tropical highland species, without propagula, then the propaguliferous species will have to bear the name *B. cancellata,* which antedates the long-established and well-known name *B. Jooriana.*

I have not been able to see the type material of *Desmatodon Bushii* Card. & Thér. from Missouri (1904), but can place it here without much question, from the description, especially from the remark that the peristome is to be compared with that of *B. cancellata.*

18. Barbula cylindrica (Tayl.) Schimp. in Ruthe, Hedwigia **12:** 46. 1873.

Zygotrichia cylindrica Tayl. in Mackay, Fl. Hib. **2:** 26. 1836.
Tortula cylindrica Lindb., Bot. Not. **1865:** 76. 1865.
Barbula flexifolia Hampe, Linn. **30:** 456. 1860.
B. subfallax C. Müll., Bot. Zeit. **20:** 338. 1862.
B. insulana Husn., Mouss. N. Ouest. **81:** 1873.
B. Beecheyi Lesq. in Watson, Bot. Calif. **2:** 372. 1880.
B. vinealis Brid. var. *cylindrica* Boulay, Mouss. Fr. **430.** 1884.
B. subcylindrica Broth., Bot. Centralbl. **44:** 387. 1890.
B. robustifolia C. Müll. & Kindb. in Macoun, Cat. Canad. Pl. **6:** 56. 1892.
B. circinnatula C. Müll. & Kindb. in Macoun, Cat. Canad. Pl. **6:** 56. 1892.
B. tortellifolia C. Müll. & Kindb. in Macoun, Cat. Canad. Pl. **6** 56. 1892.
B. horridifolia C. Müll. & Kindb. in Macoun, Cat. Canad. Pl. **6:** 57. 1892.
B. pseudorigidula Kindb. in Macoun, Cat. Canad. Pl. **6:** 264. 1892.

This species, when well developed, is apt to be confused with none of our other species except, perhaps, *B. rubiginosa* Mitt., from which it is easily distinguished by the very different areolation, flexuous leaves, and the presence of a peristome. However, there is a very wide range of variation in *B. cylindrica*, as the extensive synonymy shows. Some of the specimens from Washington and British Columbia are much larger than any of the European specimens I have seen, whereas other specimens from farther south are much smaller and approach *B. vinealis* Brid. very closely. Apparently the fundamental differences between *B. cylindrica* and *B. vinealis* are as much quantitative as strictly qualitative, and no single

morphological characteristic is limited exclusively to either one species or the other. In general, the longer and more flexuous leaves, which are less strongly revolute, and the more papillose leaf cells, which are also smaller, will serve as identifying marks for *B. cylindrica*.

19. *Barbula decursivula* Kindb. in Macoun, Cat. Canad. Pl. **6**: 264. 1892.

The type material of this species, which the author compared to *B. brachyphylla* Sulliv., is without much doubt a somewhat reduced form of *B. fallax* Hedw., as is shown by the leaf shape, areolation, and particularly by the elongated cells which make up the ventral surface of the costa. The type collection of *B. decursivula*, which occurred "On earth, on rocks at Hector, Rocky Mountains, August 15th, 1890" thus represents one of the westernmost stations for *B. fallax*.

20. *Barbula Dieckii* Broth., Hedwigia **32**: 262. 1893. (*Didymodon Dieckii* Kindb., Eur. & N.-Amer. Bryin. **278.** 1897)

The type material of this species, from Washington, was compared to *Didymodon tophaceus* (Brid.) Jur. by Brotherus, but almost certainly belongs to *B. rubiginosa* Mitt. Although the type specimens are sterile, the plants have the characteristic colors, being yellowish-green above, but black below, and the leaves have the extremely uniform basal areolation of *B. rubiginosa*. The fact that the type locality is in Washington lends additional support to this view, as *B. rubiginosa* is most common in northern Washington and southern British Columbia.

21. *Barbula Donnellii* (Aust.) Lesq. & James, Manual. **128.** 1884.

The type material of Austin's *Tortula Donnellii*, from Florida, consists of a mixture of *Barbula agraria* Hedw. and *Desmatodon Sprengelii* (Schwaegr.) R. S. Williams. Dr. A. J. Grout has decided (*in litt.*) that Austin, already familiar with the *Barbula*, intended the new name for the *Desmatodon*, so that *Barbula Donnellii* should go into synonymy under *Desmatodon Sprengelii*. In spite of the statement in Lesquereux and James' "Manual" (1884, p. 128) that *B. Donnellii* is "Apparently a variety of one of the two preceding species" (*B. agraria* Hedw. and *B. Raui* Aust.), evidence for Dr. Grout's disposition of it is given by the remark in the "Manual" (l.c.) that *B. Donnellii* has "Leaves involute, . . . obscurely serrulate at the apex," since neither characteristic applies to *B. agraria*.

The material of *B. Donnellii* which has been issued in various exsiccati is almost generally *B. agraria*.

22. Barbula Ehrenbergii (Lor.) Fleisch., Musci Archipelagi Indici Ser. IV, No. 161. 1901.

Trichostomum Ehrenbergii Lor., Abhandl. K. Akad. Wiss. Berlin **1867:** 25. 1868.

To Mr. Bartram must go the credit for recognizing this species within our range. Probably many specimens of it are to be found in the larger herbaria, misplaced under *Trichostomum* or *Didymodon*, both of which it resembles in several ways. In Mr. Bartram's herbarium are specimens from Texas, Oklahoma, and Missouri, which indicates that the species is apt to turn up elsewhere in the south and west.

The taxonomic position of this species has always been somewhat of a puzzle, until recently, when fruiting specimens of a very closely related plant were described from British Honduras (Steere, 1938a). Although the British Honduras material is enough different in gametophytic characteristics so that it cannot be safely thrown into *B. Ehrenbergii*, still it is sufficiently closely related to indicate the probable peristome structure. The peristome is quite typical of the genus *Barbula*, and exceedingly fragile, so that the teeth and even the low basal membrane are soon lost, giving deoperculate capsules a convincing appearance of being completely and naturally gymnostomous. That more typical material of *B. Ehrenbergii* behaves in a parallel manner is shown by the fact that the species has recently been placed in the gymnostomous genus *Hyophila* (Mönkemeyer, 1928). Of course, it cannot be placed in either *Trichostomum* or *Didymodon* (as has been proposed), because of the spirally twisted teeth.

23. *Barbula elata* Dur. & Mont. in C. Müll., Syn. Musc. **1:** 620. 1849.

This species, originally described from Algeria, has not yet been recognized in Europe; at least a search of the major monographic treatments of the European moss flora does not reveal even the name. In spite of the restriction of *B. elata* in the eastern hemisphere to Algeria, it has been reported from California, on the basis of Bolander's collections, by Lesquereux and James (1884), with the following remarks: "Near San Francisco (Bolander), mixed with the two preceding species [*B. virescens* Lesq. and *B. cylindrica* (Tayl.) Schimp.]. The more distant leaves, less open, recurved when moist, the stem-leaves ovate, decurrent at base, and especially the larger, broader capsule with longer, twice-twisted teeth, etc., separate this species from *B. vinealis*. The above description [i.e., of *B. elata* in the 'Manual'] made from the examination of a large number of specimens, slightly differs from that of Mueller. But this author has compared specimens and confirmed their identity with the foreign plant."

There is no real phytogeographic incompatibility in the discovery of an otherwise endemic Algerian species in California, as the climates of the two regions are essentially rather similar. The occurrence of *B. elata* in

the moister parts of Montana, Washington, and Oregon, reported by later workers, even as reliable as Brotherus (1893), would seem to be a bryogeographical impossibility, of course. Examination of specimens from the American northwest has shown them to be, beyond doubt, only *B. cylindrica* (Tayl.) Schimp. It is more than probable that Bolander's "*B. elata*" was the same, especially when Lesquereux and James' remark is recalled, that it was growing in mixture with *B. cylindrica* and *B. virescens*, the latter being a synonym of *B. vinealis*. Most of the specimens of "*B. elata*" from California, in various herbaria, are either *B. cylindrica* or *B. vinealis*.

The Herbarium of the New York Botanical Garden contains an interesting collection which bears on the packet, in ink, the following inscription: "*Tortula elata*, Dav. et Mont.—Algeria.—April 1848." Under the ink, however, is a faintly pencilled legend, apparently in the characteristic hand of Mrs. Britton, which sheds somewhat more light on our problem. In the first place, the pencilled spelling of the authorities is correct. In the second place, the last digit in the date, which is inked in as "8" is, in pencil, almost certainly a carelessly made "0." The reason for this careful documentation is that in the description of *Tortula elata* Dur. et Mont. (Montagne, 1849) which appeared at about the same time as (or earlier than?) Müller's description of *Barbula elata* Dur. & Mont., the habitat is given as "Ac rupas rivuli radices collis *Tournit* sublentis aprili 1840 in Algeria detexit cl. Durieu." Thus, the specimen in the New York Botanical Garden is almost conclusively proved to be a part of the type collection, or at least authentic material. Consequently, the determination of its status is a very critical matter. The leaves are long and flexuous, especially at the apex of the stem. The capsules are old, deoperculate, and have lost the peristome. Nevertheless, I do not hesitate in pronouncing this material to be a form of *B. cylindrica* (Tayl.) Schimp., without any reasonable doubt. The name *Barbula elata* must no longer be used for American specimens, and if the collection described above represents type material, the name cannot be used for the Algerian material, either.

24. BARBULA EUSTEGIA Card. & Thér., Bot. Gaz. **30**: 17. 1900.
B. perannulata Williams, Bull. N. Y. Bot. Gard. **2**(7): 358. 1902.

The type specimen of this species came from Cedar Creek, Latah County, Idaho. It has since been collected in Washington, Montana, and Utah. From the large number of specimens collected by Flowers and Garrett in Utah, especially in the Wasatch Mountains, it appears that this species is more common and abundant there than *B. convoluta*, from which it differs most conspicuously in the costate perichaetial leaves with a long, papillose apex or apiculus.

B. eustegia rather resembles the European *B. flavipes* Bry. eur., and it may eventually be necessary to place it there. However, the whole plant, in all its parts, is much smaller; furthermore, the perichaetium of *B. eustegia* is of fewer leaves, and much smaller in relation to the stem leaves, which may sometimes surpass it.

The sporophyte of *B. eustegia* is very similar to that of *B. convoluta* Hedw. Jones (1929) attempted to separate the two species in his key by the comparative lengths of the rostrate operculum, indicating that the operculum of *B. convoluta* is less than one half the length of the urn. Actually, however, in many specimens of *B. convoluta*, the operculum is longer than the urn, exactly as in *B. eustegia*.

25. Barbula fallax Hedw., Sp. Musc. **120.** 1801.

B. acuminata Hedw., Sp. Musc. **117.** 1801.
B. sparsidens C. Müll. & Kindb. in Macoun, Cat. Canad. Pl. **6**: 54. 1892.
B. decursivula Kindb. in Macoun, Cat. Canad. Pl. **6**: 264. 1892.

This species has been very commonly considered to be widespread in our range from coast to coast, and every herbarium has its quota of specimens from the Pacific Coast states, especially California. In spite of this long-established idea, the specimens from the west coast attributed to *B. fallax* all belong actually to other species, usually *B. vinealis*.

B. fallax is really an eastern species, widespread from Nova Scotia to Virginia, west to Iowa and Minnesota. Farther west, the species seems much rarer and specimens are usually atypical, although a few reasonably typical specimens have come from Montana and Idaho. The two British Columbia collections described by Kindberg as two new species, *B. decursivula* and *B. sparsidens*, are much reduced, the first one so much that it is hardly recognizable as *B. fallax*.

Although *B. fallax* is rather variable, it (and its allies, *B. reflexa* (Brid.) Brid. and *B. michiganensis* Steere) may be easily separated from *B. vinealis* Brid., the species with which it is usually confused, by an easily observed and clear-cut characteristic, namely, the elongated cells (in surface view) composing the ventral surface of the costa. Furthermore, the peristome is of a clear, bright red, and does not become paler with age.

26. *Barbula flexifolia* Hampe, Linn. **30**: 456. 1860.

The type collection of this species (from California) is a small form of *B. cylindrica* (Tayl.) Schimp. Concerning *B. flexifolia*, Lesquereux and James (1884) very appropriately remark: "This and other species of the *B. vinealis* group are most difficult to separate, and their number may be either reduced or indefinitely increased." Renauld and Cardot (1896), in

the same vein, say of this species: "C'est une des nombreuses formes américaines du groupe des *B. vinealis* et *cylindrica*, que l'on à élevées au rang d'espèces, mais dont la valeur nous semble fort problématique. Une étude attentive de ce groupe conduira sans doute à y opérer de nombreuses réductions." In spite of many other remarks of the same sort which have appeared in the literature, none of the authors have taken the trouble to go ahead and straighten out the confusion which they suspect.

27. *Barbula gracilis* Schwaegr., Sp. Musc. Suppl. **1**(1): 125. 1811.

The name *B. acuta* (Brid.) Brid. (Method. Musc. **96.** 1822) must be used for this species instead of *B. gracilis*, which is preceded by *Tortula acuta* Brid. (Musc. Recent. Suppl. **1:** 265. 1866).

28. *Barbula horridifolia* C. Müll. & Kindb. in Macoun, Cat. Canad. Pl. **6:** 57. 1892.

The type specimens of this species, from "Damp rocks, near the whirlpool, west of the Columbia River, at Revelstoke, B. C." without doubt represent only a large form of *B. cylindrica* (Tayl.) Schimp. which has been so often redescribed under different names by Müller and Kindberg.

29. Barbula icmadophila Schimp., Bry. Eur. fasc. **43,** suppl. II. 1850.

This species is recognized with any reasonable certainty in North America from only two specimens, in spite of several published reports and many collections so named in herbaria. The two collections which I should place here are R. S. Williams' *No. 143a* from Columbia Falls, Montana, and the admixture in Drummond's "Musci Americani" *No. 139*, issued as *T. fallax*. Although both specimens differ from European material in the somewhat papillose cells and shorter stems, they agree pretty well otherwise. In fact, Mitten (1878) has said of Drummond's collection just cited: " . . . fine specimens with fruit were in some sets of Drummond's Musci Americani, *No. 139*, as *T. fallax*, from banks of rivers near the Rocky Mountains." In the same place, Mitten reports "a few small barren stems" of *B. icmadophila* among other mosses at two stations in the extreme northernmost part of the Canadian Arctic Archipelago, at Floeberg Beach, Lat. 82°27′ N., and at Mushroom Point, Lat. 82°29′12″ N., on the north coast of Ellesmere Island. I have not seen these specimens from the English Arctic Expedition of 1875–1876, and so cannot express an opinion on them. For some reason, they are not in the Mitten Herbarium. now in the possession of the New York Botanical Garden.

30. *Barbula indigens* (Ren. & Card.) Ren. & Card., Bull. Soc. Roy. Bot. Belg. **36**(2): 176. 1897. (*Trichostomum indigens* Ren. & Card., Bot. Gaz. **4:** 50. 1896.)

Type material of this species, from Newfoundland, is almost certainly a much reduced form of *B. unguiculata* Hedw., with which it is compared by the authors. *B. unguiculata* apparently reaches its northern limit in eastern North America in Newfoundland, and since reduction in size is so typically concomitant with distribution in high latitudes, in species characteristic of temperate climates, it should not be taken as an excuse for the proposal of new species. At the other end of our geographical range, Cardot made the curious error of applying the name *B. indigens* to rather typical specimens of *B. Cruegeri* Sond. collected at Columbia, Texas, and to unquestonable *B. unguiculata* from Missouri. This extremely disjunct geographical range should have aroused suspicion as to the validity of the species, even before a critical examination of authentic material.

31. *Barbula insulana* (DeNot.) Husn., Mouss. nord-ouest **81.** 1873.

This name, which is a synonym of *B. cylindrica* (Tayl.) Schimp., has been applied to American plants and so has appeared a few times in the literature concerning them.

32. BARBULA JOHANSENII Williams, Rept. Canad. Arct. Exped. 1913–18. 4(E): 4. 1921.

As this species is known only from the nearly inaccessible type locality, Murray Point, Victoria Island, Arctic Northwest Territory, Lat. 68°40′ N., on dolomite cliffs (Frits Johansen, March 25, 1916), and only from one small collection, it must be admitted to our flora with some question. However, it seems to be distinct, although closely related to *B. acuta* (Brid.) Brid., and certainly differs from every other species in the genus in the swollen, caducous apex of the costa, which must serve in some way for vegetative reproduction.

33. *Barbula Jooriana* C. Müll., Bull. Torrey Bot. Club **5**(12): 49. 1874.

The type specimen (from Baton Rouge, Louisiana) of this species has been seen, through the kindness of the Botanical Museum, Berlin-Dahlem, Germany. It represents, without question, *B. Cruegeri* Sond., since axillary propagula are present, although not particularly well developed. Many bryologists from the time of the Lesquereux and James' "Manual" (1884) on have considered *B. Jooriana*, under which name the majority of specimens of *B. Cruegeri* pass, most closely related to *B. unguiculata* or even not separable from it.

34. *Barbula lanceolata* Hedw., Sp. Musc. **119.** 1801.

In the original description, according to which the type collection was found growing "Terrestris Lancastriae in Pensilvania," Hedwig gave no

indication as to what he considered the affiliations of his new species. Cardot (1899), however, has examined the original material and pronounced it to be a form of *B. unguiculata* Hedw.

35. *Barbula lateritia* Kindb., Eur. & N.-Amer. Bryin. **264.** 1897.

Type material of this species, as nearly as the type material of any of Kindberg's species may be ascertained, although sterile, is a short form of *B. vinealis* Brid., which approaches *B. brachyphylla* Sulliv. rather closely, especially in the leaf margins revolute from the base nearly to the apex.

36. *Barbula melanocarpa* C. Müll. & Kindb. in Macoun, Cat. Canad. Pl. **6**: 54. 1892.

The type material of this species, from Yale, B. C., certainly represents *B. rubiginosa* Mitt. The complete lack of any peristome, the absolutely characteristic basal areolation of the leaf, and the curious, almost metallic blackness of the old leaves identify it beyond question.

37. Barbula michiganensis Steere in Grout, Moss Fl. N. Amer. **1**(3): 180. 1938.

This species, although known only from the type locality on the south shore of Lake Superior, is represented by several collections made at different times, and seems distinct enough to necessitate recognition. The very thick-walled, seriate cells of the lamina, the elongated cells of the ventral surface of the costa, as well as the whole general appearance of the plant, especially the catenulate leaf arrangement when dry, all point to a definite relationship with *B. fallax* Hedw. However, the clasping, erect leaf base, with only the apex reflexed- and erect-spreading, is very different from the widely reflexed-spreading leaf arrangement in *B. fallax* and, still more, in *B. reflexa* (Brid.) Brid. Also, the cells are thicker walled, less papillose, and much more conspicuously arranged in parallel rows than usual in *B. fallax.* The really unique feature, however, is the presence in large numbers of reddish, spherical, multicellular propagula in the axil of each leaf, because this type of propagulum is not known in any other of our American species, nor have propagula of any type been reported for either *B. fallax* or *B. reflexa.*

38. *Barbula oenea* C. Müll. & Kindb. in Macoun, Cat. Canad. Pl. **6**: 55. 1892.

An examination of the sterile type specimen of this species shows it to be almost certainly a *Didymodon*, as the authors themselves suspected. Just what species is represented would be very difficult to say, however,

as the type material is not only very scanty, but also poorly developed. It was growing, according to the authors, on soil subject to inundation, a variable habitat which has left its mark upon the specimens. This name should be discarded altogether, without hesitation.

39. *Barbula perannulata* Williams, Bull. N. Y. Bot. Gard. **2**(7): 358. 1902.

The original material of this species came from Montana and Idaho. An examination of the type specimens, the original description, and Williams' illustrations leaves no reasonable doubt that it is a question of *B. eustegia* Card. & Thér., which was described from the same general region only two years earlier.

40. BARBULA PLATYNEURA C. Müll. & Kindb. in Macoun, Cat. Canad. Pl. **6**: 52. 1892.

In this plant, C. Müller and Kindberg seem actually to have found a valid new species. After seeing specimen after specimen of well-known and long-established species wrongly identified and badly confused, or, still worse, proposed as innumerable new species, one develops a certain distrust of Kindberg's reliability. However, although this species is still known only from the type specimen, it is different from any other species and is seemingly the American counterpart of the European *B. Hornschuchiana* Schultz, from which it differs in its tendency toward a more obtuse leaf apex and the lack of spiral twisting of the leaves when dry. From *B. spiralis* Schimp., of the arid southwest, it differs in smaller size, more acute leaves, and the much shorter basal leaf cells.

41. *Barbula pseudorigidula* Kindb. in Macoun, Cat. Canad. Pl. **6**: 264. 1892.

The type material of this species is without much doubt a form of *B. cylindrica* (Tayl.) Schimp. with which it agrees in the flexuous leaves, spreading when moist, and in "the peristome pale and distinctly contorted." In just these same characteristics it differs from *B.* (*Didymodon*) *rigidula*, which also has the upper leaf margins thickened.

42. *Barbula purpurea* C. Müll., Flora **58**: 78. 1875.

Sullivant and Lesquereux's "Musci Boreali-Americani" *No. 135* (Ed. II), issued as *B. brachyphylla* Sulliv., is in part the type material of this species. I have seen several separate packets of *No. 135*, from different sets, as well as the actual material selected out by Müller, from his herbarium. The species is apparently only a habitat variation of *B. brachyphylla* and not enough different to justify separation from it.

43. *Barbula Raui* Aust., Bull. Torrey Bot. Club **6**: 43. 1875.

Although this species has been considered as valid and distributed in exsiccati even since 1930 (for instance, *No. 194* of Grout's "North American Musci Perfecti"), I am obliged, after an examination of the type specimen, to agree with Mrs. Britton (1913) and Williams (in herb.) that it is too close to *B. agraria* Hedw. for recognition, and so should go into synonymy under *B. agraria*.

44. *Barbula Ravenelii* Aust., Bot. Gaz. **2**: 89. 1877.

The original specimens upon which this species was based, although somewhat reduced, are typical *B. Cruegeri* Sond., even to the well-developed axillary propagula. *B. Cruegeri* must be rare in Georgia, because, although the type specimen of *B. Ravenelii* was collected prior to 1877, no other specimens from Georgia have found their way into the larger herbaria.

45. *Barbula recurvifolia* Schimp., Coroll. Bry. Eur. **33.** 1855.

This name is preceded by *B. reflexa* (Brid.) Brid. (Method. Musc. **93.** 1822), which, then, is the proper one to use.

46. Barbula reflexa (Brid.) Brid., Method. Musc. **93.** 1822.

This species, subspecies, variety, or form, as it has been variously considered by as many authors, is very closely related to *B. fallax* Hedw., and has much the same geographic range. It is not particularly variable, and differs fairly consistently from *B. fallax* in its redder color, more papillose leaf cells, and more strongly recurved or even squarrose leaves. As to the proper category in which to place this moss, it is probably best considered a "small" species or a subspecies of *B. fallax*.

47. *Barbula rigens* Card. & Thér., Proc. Wash. Acad. Sci. **4**: 305. 1902.

The type material of this species, from Alaska, consists of only a few sterile stems, which, although puzzling, seem to represent an elongated, underdeveloped form of *Didymodon recurvirostris* (Hedw.) Jennings (*D. rubellus* Bry. eur.). This view is based upon the very typical coloration, the much elongated basal cells and the costa shortly excurrent into a minute, pellucid apiculus. The apical teeth are very poorly developed, however, although they may commonly be lacking or poorly developed in specimens from more Arctic regions.

48. *Barbula rigidula* (Hedw.) Milde, Bryol. Siles. **118.** 1869.

This species, although closely related to *Barbula* in appearance and habitat, is to be kept in the almost completely synthetic genus *Didymodon* (Steere, 1938c) as long as it is maintained, on the basis of the nearly

straight peristome teeth and the fact that it is the type species of Hedwig's genus *Didymodon*. It is worth remarking here that, although Mitten (1867) is almost universally given credit for the transfer of this species to *Barbula*, he, in the place always cited, speaks only of "*T. rigidula*," although he does make the following qualifying remark at the beginning of his paper: "In Britain these mosses are, for the most part, called *Tortulas*, but elsewhere they are found in Bryological works, generally under the synonymous name of *Barbula*, which later designation they may probably eventually retain when the present chaotic state of the extensive family, of which they form a part, shall have been reduced to order on some more natural plan; a few species have been placed in *Trichostomum* and *Didymodon*, from the importance which has been placed in the length of the peristome teeth." The expression of this viewpoint can hardly be construed as establishing a valid new combination, and as Mitten nowhere uses "*Barbula rigidula*" he can not very logically be cited as the authority for it. Milde, in the work cited above, seems to have first used this combination, insofar as I can discover, and so it should be attributed to him, if the species be retained in *Barbula*.

49. *Barbula robustifolia* C. Müll. & Kindb. in Macoun, Cat. Canad. Pl. **6**: 56. 1892.

The type specimens of this species, from Vancouver Island, are simply a robust form of *B. cylindrica* (Tayl.) Schimp. into which it should be thrown.

50. Barbula rubiginosa Mitt., Journ. Linn. Soc. Bot. **8**: 27. 1865.

Barbula subicmadophila C. Müll. & Kindb. in Macoun, Cat. Canad. Pl. **6**: 53. 1892.

B. melanocarpa C. Müll. & Kindb. in Macoun, Cat. Canad. Pl. **6**: 54. 1892.

B. Dieckii Broth. in Röll, Hedwigia **32**: 262. 1893.

Didymodon Dieckii Kindb., Eur. & N.-Amer. Bryin. 278. 1897.

Although this species seems to be especially common along the Columbia River, it is widespread in Oregon, Washington, Idaho, Montana, and southern British Columbia. It has often been confused with *B. cylindrica* (Tayl.) Schimp., quite unreasonably. Fertile specimens are absolutely unique in their complete lack of any peristome. Sterile specimens are also easily recognized by the more decurrent leaves, which are less contorted when dry and less flexuous when moist, as well as by the extremely uniform, short basal leaf cells, which may actually be wider than long. The relationships of this species in the genus *Barbula* are very obscure. I find myself somewhat in sympathy with Kindberg (1897), who placed it in *Didymodon*. Of course, the total lack of a peristome and the peculiar areo-

lation are known otherwise in neither *Barbula* nor *Didymodon*. If these characteristics are of any real taxonomic importance, then perhaps it may eventually be necessary to erect a new genus to contain this species.

51. *Barbula Saundersii* Card. & Thér., Proc. Wash. Acad. Sci. **4:** 304. 1902.

The original material upon which this species was based, from southern Alaska, "in habit recalls the smallest forms of *B. unguiculata* Hedw." The characteristic dirty green color, the basal areolation of the leaf, and the costa papillose on the back substantiate the authors' suspicion that this might represent *B. unguiculata*. The shape of the leaf is rather different, as the authors point out. However, in a species as polymorphic as *B. unguiculata*, variants of this sort hardly merit recognition, even with the rank of a form. This is especially true of specimens such as these, from the extreme northern limit of the geographic range, where the climate may naturally be expected to influence a species of temperate regions.

52. *Barbula semitorta* Sulliv., Rept. Pacific R. R. Survey (35th Parallel) **4:** 186. 1856.

The Californian specimens upon which this name is based are clearly a form of *B. vinealis* Brid., which, as the author states, accompanies it.

53. *Barbula sinuosa* (Wils.) Jaeg., Adumb. **1:** 286. 1873.

In the first place, this species is probably not a *Barbula* at all: at least that is my conclusion after studying several European collections. In the second place, the species, whether or not it belongs to *Barbula*, apparently does not occur in North America, in spite of published reports to the contrary by Kindberg and others.

54. *Barbula spadicea* (Mitt.) Braithw., Brit. Moss-Fl. **1:** 266. 1887.

This species is not particularly closely related to, but often confused with *Didymodon rigidulus* Hedw., and the remarks which have been made concerning the latter species also apply here. The straight or nearly straight peristome teeth force its inclusion in the genus *Didymodon*, for the present at least. For the sake of exactitude in citation, however, it might be mentioned that in the original description this species was proposed unequivocally and unmistakably as a *Tortula* by Mitten (1867). Nevertheless, most bryologists have credited Mitten with the authorship of the name *Barbula spadicea*, although citing the place of publication of his "*T. spadicea*, n. sp."; perhaps because of his qualifying remarks already quoted under *B. rigidula*. So far as I can find, Braithwaite, as cited above, was the first to use the actual combination *Barbula spadicea*, although he himself indicated Mitten as the author.

55. *Barbula sparsidens* C. Müll. & Kindb. in Macoun, Cat. Canad. Pl. **6**: 54. 1892.

The authors say of this species in the original description: "Allied to *B. fallax*, but differing principally in the peristomial teeth, spreading, loosely, and not spirally twisted." A careful examination of the type specimens, from "Along the west side of the Columbia River, at Revelstoke, B. C." has shown them not only to be reasonably typical *B. fallax* Hedw., but also to be from the westernmost outpost of that species. When the operculum is first removed or the teeth are moistened, they assume the characteristic spiral contortion. In old, dry peristomes the teeth spread out, giving the false appearance of being untwisted. The clear, deep red color of the peristome and the elongated cells composing the ventral surface of the costa complete the identification of this species with *B. fallax* beyond question.

56. Barbula spiralis Schimp. in C. Müll., Syn. Musc. **1**: 622. 1849.

Concerning the distribution of this species, Bartram (1927) says: "This species is apparently quite common in the elevated districts of central Mexico and is certainly not uncommon in Arizona where it has been collected in a number of localities, usually on dry banks in the foothills of the border mountain ranges. Collections by Mr. Holzinger in New Mexico and by Mr. C. R. Orcutt in western Texas indicate that the species probably occurs throughout the arid southwest at elevations around 5000 feet."

From *B. platyneura* C. Müll. & Kindb., its closest relative, *B. spiralis* is separated easily by the larger size and less acute leaves, but especially by the much longer basal leaf cells. It seems to be related to the European *B. revoluta* Brid., but differs in the much larger size and undifferentiated perichaetial leaves. I have not seen any material with sporophytes from our range.

57. *Barbula stricta* Hedw., Sp. Musc. **119**. 1801.

Cardot (1899) examined the type material of this species, which, according to the original description, came from "Lancaster Pensilvaniae, terrestris," and has pronounced it to be a robust form of *B. unguiculata* with tall stems.

58. *Barbula subandreaeoides* Kindb., Rev. Bryol. **32**: 36. 1905.

The original material upon which this name was based, from the western slope of the Rocky Mountains, British Columbia, rather definitely represents a form of *Andreaea Rothii* Web. & Mohr, a conclusion which Dr. Sharp has confirmed.

59. *Barbula subcylindrica* Broth., Bot. Centralbl. **44**: 387. 1890.

Through the kindness of Dr. K. Linkola, of the Botanical Institute of Helsinki University, I have seen type specimens from Brotherus' Herbarium. In spite of the slight deviations from typical *B. cylindrica* (Tayl.) Schimp. noted by the author, the type material falls well within the range of variation of the American forms of *B. cylindrica*.

60. *Barbula subfallax* C. Müll., Bot. Zeit. **20**: 338. 1862.

The type material of this Californian species, which has been seen through the kindness of the Berlin-Dahlem Botanical Garden, clearly represents a somewhat reduced form of *B. cylindrica* (Tayl.) Schimp., in spite of the comparison with *B. fallax* Hedw. by the author. The leaves are crowded, longer, and flexuous at the stem apex, the leaf margin is not revolute above the middle, and in all other critical features it agrees with *B. cylindrica*.

61. *Barbula subgracilis* C. Müll. & Kindb. in Macoun, Cat. Canad. Pl. **6**: 53. 1892.

Although the authors consider this species "allied to *B. gracilis*," several of the characteristics mentioned in the original description distinctly contradict such an alliance. For instance, the "leaves when dry subcrispate, when moistened squarrose, curved from the ovate base" are not at all characteristic of *B. acuta* (Brid.) Brid., but of the *B. vinealis* Brid. series. A study of the type specimens has shown them to represent *B. vinealis*.

62. *Barbula subicmadophila* C. Müll. & Kindb. in Macoun, Cat. Canad. Pl. **6**: 53. 1892.

The original material of this species, from "dry rocks, but which are covered at high water, at Yale, B. C." is certainly *B. rubiginosa* Mitt. The complete lack of a peristome, in the first place, is the most positive means of identification.

63. *Barbula tortellifolia* C. Müll. & Kindb. in Macoun, Cat. Canad. Pl. **6**: 56. 1892.

The type specimens upon which this species was based, from various parts of British Columbia, are clearly the same large form of *B. cylindrica* (Tayl.) Schimp. which these authors chose to redescribe so many times as different species.

64. *Barbula Treleasei* Card. & Thér., Proc. Wash. Acad. Sci. **4**: 305. 1902.

In spite of the authors' comment on this species: "It differs from *B.*

vinealis Brid., and allied forms, by the much shorter leaves," the type material, from Juneau, Alaska, is rather typical *B. vinealis*, even to the single pellucid cell at the apex of the leaf.

65. Barbula unguiculata Hedw., Sp. Musc. **118.** 1801.

Barbula indigens (Ren. & Card.) Ren. & Card., Bull. Soc. Roy. Bot. Belg. **36**(2): 176. 1897.

B. Saundersii Card. & Thér., Proc. Wash. Acad. Sci. **4**: 304. 1902.

The typical American form of this extremely common, widely distributed, and variable species differs from the typical European form in the less strongly excurrent costa, which forms a shorter mucro, and in the less hyaline basal cells, as well as in more subtle and less easily defined ways. Yet the two forms are united by a whole series of intergrading forms. Many variants, whose names reveal their nature, have been given formal recognition at various times in the past, as *cuspidata, apiculata, microcarpa, obtusifolia, polycarpa, fastigiata*, etc. All these merge imperceptibly with the typical form, however, and are of no real taxonomic value, even as forms.

66. Barbula vinealis Brid., Bryol. Univ. **1**: 830. 1826.

Tortula vinealis Spruce, Hook. Journ. Bot. **4**: 194. 1845.

Barbula semitorta Sulliv., Rept. Pacific R. R. Surv. (35th Parallel) **4**: 186. 1856.

B. virescens Lesq., Trans. Amer. Phil. Soc. **13**: 4. 1865.

B. cylindrica (Tayl.) Schimp. var. *vinealis* Lindb., Musc. Scand. **22.** 1879.

B. brachyphylla Sulliv. var. *angustifolia* Kindb. in Macoun, Cat. Canad. Pl. **6**: 55. 1892.

B. lateritia Kindb., Eur. & N.-Amer. Bryin. **264.** 1897.

B. Treleasei Card. & Thér., Wash. Acad. Sci. Proc. **4**: 305. 1902.

This is, without doubt, the most variable species of *Barbula*, and is represented, especially in California, by a perplexing series of races and habitat forms, too many of which have been proposed as species. Sullivant's *B. brachyphylla*, which apparently represents the most reduced state of *B. vinealis*, usually with a somewhat blunt leaf apex and with the whole leaf margin revolute, is distinct enough for recognition as a species or subspecies, in its typical form. Puzzling intermediate forms do occur, however. In the other direction, the more robust forms of *B. vinealis* intergrade to some extent with *B. cylindrica* (Tayl.) Schimp. Yet the total range of the three "species" is too great to enable us to lump them under one name. Perhaps further study will uncover better morphological and qualitative distinctions between them.

B. vinealis has long been confused with *B. fallax* Hedw., with the result that in every herbarium there are too many specimens labelled "*B. fallax*," especially from the Pacific Coast. Although there are many forms of *B. vinealis* which almost exactly duplicate the macroscopic habit of *B. fallax*, the geographical ranges hardly overlap, and under the microscope the two species are very distinct. The leaf cells of *B. vinealis* are ordinarily much less papillose and less thickened, and the peristome teeth are rarely a deep, clear red, but have a dusty or glaucous quality, and become much paler or even completely white with age. An inspection of the ventral (upper) surface of the costa under the microscope will separate the two species without any question, for in *B. vinealis* the cells are short, appearing as a continuation of the leaf blade across the costa, whereas in *B. fallax* the cells are much narrower and elongated, very different from those of the lamina.

It is interesting to read the comments made by earlier bryologists on the American species of *Barbula*, and to discover what sort of specific concepts they held, especially with reference to the perplexing *B. vinealis* group. Lesquereux (1865) was apparently distinctly puzzled, as his remarks show. Concerning *B. vinealis* Brid., he says: "Very common and variable around San Francisco. Var. α has the ramification, form of leaves, etc., of *Barbula vinealis;* but the operculum and peristome of *Barbula flexifolia*. Var. β *flaccida* Bry. Eur. has the capsule and operculum of *Barbula vinealis*, and the long-linear, lanceolate, canaliculate, open-reflexed, loosely imbricated leaves of *Barbula flexifolia*. This variety is apparently the equivalent of *Barbula elata* C. Müll." On the basis of these observations, Lesquereux would have been perfectly justified in reducing *B. flexifolia* and *B. elata* at once to synonyms of *B. vinealis* Brid. var. *flaccida* Bry. Eur., which in itself is, of course, only a synonym of *B. cylindrica* (Tayl.) Schimp. Instead of following this practical course, he maintained both species in the "Manual" (1884), which, as a result of this same uncritical procedure in all groups, is essentially only a compilation. After admitting the complexity of *B. vinealis*, he went on and described (1865) two new species of *Barbula*, *B. virescens* and *B. artocarpa*. That Lesquereux himself had serious doubts concerning the validity of his new species is clearly demonstrated by his remarks. Of his *B. virescens* he says: "This species is intermediate between *Barbula flexifolia* Hmp. and *Barbula semitorta* Sul., two species already closely related." Of *B. artocarpa*, which is clearly based on *B. vinealis*, he says: "Except for its pretty large annulus, this species would agree with *Barbula gracilis* Schw., which it exactly resembles by the ramification, the form of the leaves and of the capsule. It is also nearly related to *B. subfallax* C. Müll. [*B. cylindrica*], which has also

no annulus, and a shorter basilar membrane." No good is done by the addition of new species whose value the author himself doubts, as shown by his final statement that "It is, indeed, with some misgiving that I add two new species to this group of *Barbulae* already too much divided. But I have no other alternative but to do this, or to recall as mere varieties, a number of forms considered as species by other authors, and whose characters are of the same kind and no more definite." A few years later, Lesquereux (1868) was still undecided in his treatment of the *B. vinealis* series, saying: "The forms of this section of *Barbula* found in California are so numerous, that it will be necessary to reduce them to a few species, or to make a monograph of them, embracing more than one dozen species." Still later (1884), he says (with reference to *B. flexifolia* Hampe): "This and other species of the *B. vinealis* group are most difficult to separate, and their number may be either reduced or indefinitely increased." Unfortunately, the latter choice was made by most bryologists during the next quarter century.

When as conscientious a worker as Lesquereux recognized species other workers had based upon habitat forms and proposed new species based upon characteristics which he himself considered unreliable, it is fortunate for American bryology that Bolander's Californian mosses were not sent to Kindberg.

67. *Barbula virescens* Lesq., Trans. Amer. Phil. Soc. **13**: 4. 1864.

The original material from California, upon which this species was based, is undoubtedly a form of *B. vinealis* Brid., as just pointed out under that species.

68. *Barbula Waghornei* Kindb., Eur. & N.-Amer. Bryin. **264.** 1897.

The type specimens of this species, from Newfoundland, have an excurrent costa, as the author noted, and in addition show two other characteristics which escaped the author, but which allow the material to be identified without the least doubt as *Didymodon rigidulus* Hedw. The leaf margin is characteristically bistratose above and there are groups of the typical spherical, multicellular, stalked propagula present in the axils of the leaves.

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Pollen Longevity of Ginkgo[1]

EARL H. NEWCOMER

(WITH FOUR FIGURES)

Pollen was collected May 15, 1937, from a male tree of *Ginkgo biloba* growing near the campus of The Pennsylvania State College. The primary purpose of the collection was to secure an adequate amount of pollen for germination studies by a method devised by the author for the pollen of Angiosperms (*2*). The presence of functional chloroplasts in the male gametophyte of *Ginkgo* seemed to offer favorable material for observing the fate of the plastid through a critical part of the life cycle. However, all attempts to germinate the pollen failed, although efforts were made at regular intervals for a period of more than four months with a variety of media and stimulatory substances. The apparent continued viability of the pollen for so long an interval suggested the experiment to determine its longevity.

Horsford (*1*) kept the pollen of *Lilium auratum* viable for a year by simply wrapping it in two or three sheets of paraffin paper and storing it in a warm dry place. More recently, Pfeiffer (*3*) made a detailed study using a variety of salts and acids to control humidity in conjunction with various temperatures and pressures and succeeded in keeping the pollen of *Lilium* viable for a period of fourteen months.

The *Ginkgo* pollen, which had been intermittently kept in a refrigerator at 7 degrees C. when not on the author's desk, was placed in a desiccator over powdered $CaCl_2$ as shown in figure 4, and returned to the refrigerator until the following spring. On May 2, 1938, the pollen was applied with a camel's hair brush to the young ovules of a female *Ginkgo* tree. The young ovules were bagged before pollination and subsequently for more than a month—a precaution doubtless unnecessary as the nearest male tree is a quarter of a mile distant to the leeward and wind pollination has never been observed on this tree.

That the pollen was still viable is attested by the accompanying figures of fruits taken at intervals throughout the summer. Sections of these young developing ovules and embryos show normal development.

This same tree was hand pollinated on May 15 the preceding year and cytological studies demonstrated fertilization occurring between the 5th and 20th of September. Counting this four-month period between pollination and fertilization, the pollen maintained its viability for a period of nearly sixteen months.

[1] Contribution from the Department of Botany, Michigan State College.

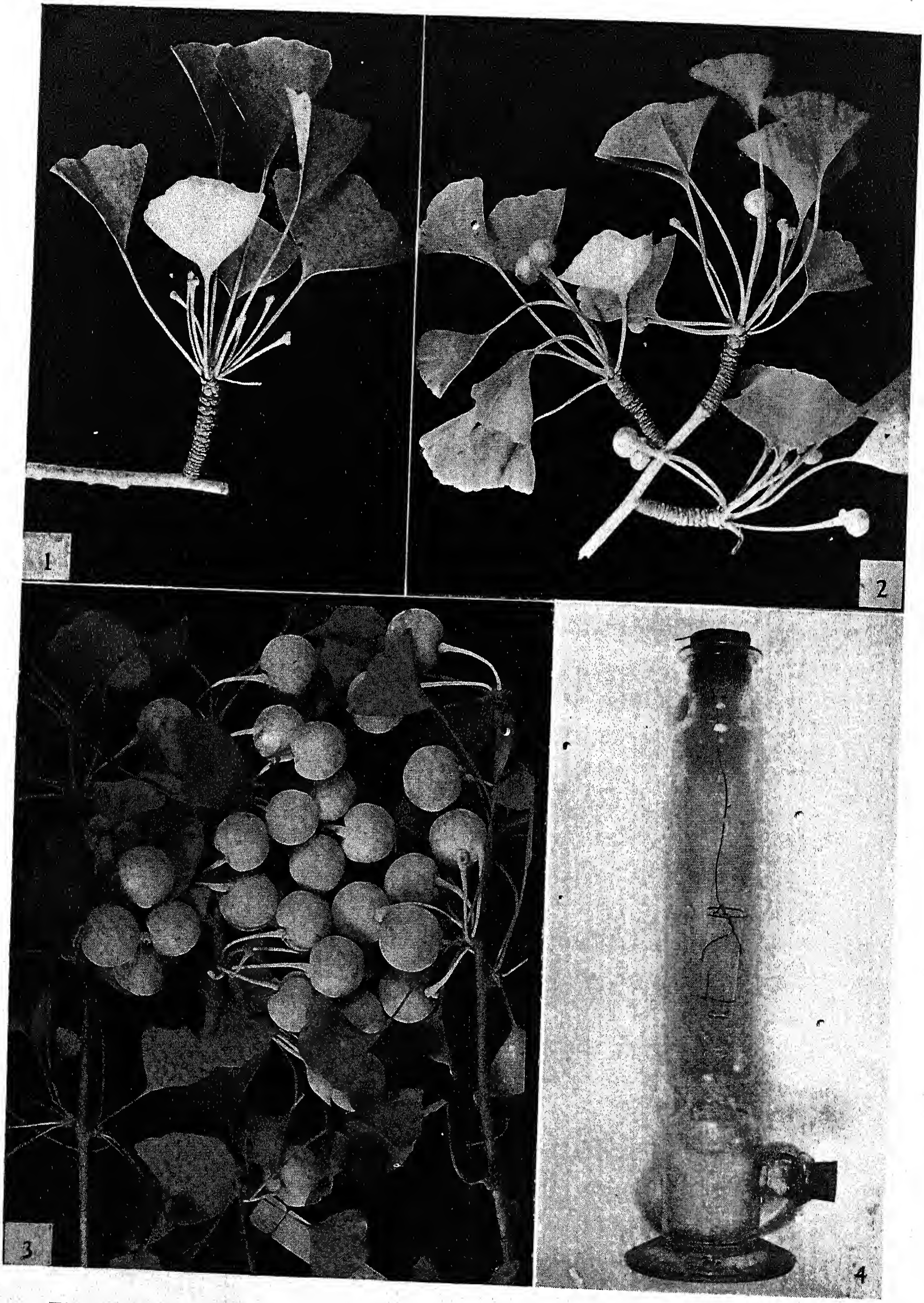

Fig. 1. Young ovules of *Ginkgo biloba* at time of pollination. May 2, 1938.

Fig. 2. Developing ovules on June 20, 1938. Abortive or unpollinated ovule in center of field.

Fig. 3. Mature fruit at time of final collection. Oct. 1, 1938.

Fig. 4. Desiccator used for storage of pollen. Vial containing pollen suspended from cork by copper wire over $CaCl_2$.

Actual percentage germination studies of viable pollen were impossible to make, but microscopic examination of the pollen at time of pollination revealed less than 1 per cent of shrivelled pollen. Indeed, present examination shows the pollen grains to be but slightly shrunken and when mounted in a drop of water, they immediately expand to their normal size and, with the exception of the almost complete disappearance of the chloroplasts, appear normal. Brownian movement of small bodies which may be the remnants of the plastid stroma, is conspicuous. The prothallial, tube and generative nuclei are still normal in appearance and position. An adequate amount of pollen remains for further experiment in the spring.

It is a pleasure to acknowledge the assistance of Professor L. O. Overholts, of The Pennsylvania State College, for the photographs, and of Dr. C. C. Wernham, of the same institution, for the final fruit collections.

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INDEX TO AMERICAN BOTANICAL LITERATURE

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Preliminary Experiments on Biotin

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(WITH ONE FIGURE)

Farries and Bell in 1930 pointed out that *Ashbya gossypii* (Ashby and Nowell) Guill. (*Nematospora gossypii* Ashby and Nowell) is unable to grow on artificial media unless small amounts of an accessory factor of the bios type are added. Buston and Pramanik (1931) established that the accessory factor is complex, consisting of at least two components one of which is meso-inositol. A second component appears to be a crystalline material isolated and studied by Kögl and Tönnis (1936) and by Kögl and Fries (1937) and named by them biotin. The empirical formula of biotin as given by Kögl (1937) is $C_{11}H_{18}O_3N_2S$; its structure is unknown.

The influence of crystalline biotin upon the growth of *A. gossypii*, as determined by Kögl and Fries, is shown in Table I. The fungus was grown 15 days at 25°C. in 25 ml. of medium containing per liter, 20 g. dextrose, 5 g. ammonium tartrate, 1 g. NH_4NO_3, 1 g. KH_2PO_4, 0.5 g. $MgSO_4 \cdot 7H_2O$, 0.1 g. NaCl, 0.1 g. $CaCl_2$, 10 drops 1 per cent $FeCl_3$ and 0.01 g. meso-inositol.

TABLE I

Effect of crystalline biotin on growth of A. gossypii[2]

BIOTIN PER FLASK GAMMA	DRY WT. MECELIUM, MG.	
		1 Gamma Thiamin
None	0.2±0.0	—
0.0001	0.6±0.0	0.7±0.0
0.001	3.1±0.1	3.2±0.2
0.01	9.8±0.1	11.0±0.2
0.1	9.1±0.3	12.3±0.3
1.0	8.7±0.2	11.5±0.1

[2] Data from Kögl and Fries.

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Although the specificity of biotin for *A. gossypii* has not been determined, Kögl and Tönnis found that biotin could not be replaced for a strain of yeast by auxin a, auxin b, heteroauxin, follicular hormone, follicular hormone hydrate, thiamin, ascorbic acid, glutathione, β-alanine, l-trysoline, l-histidine, d-arginine, dl-serine, tryptophane, l-oxyproline, glucosamine, cholin, adenine, phytin, saponin or Knight's growth vitamin for *B. sporogenes*. Until further evidence is at hand we have assumed that the growth of *A. gossypii* may be used as an indicator of the presence of biotin.

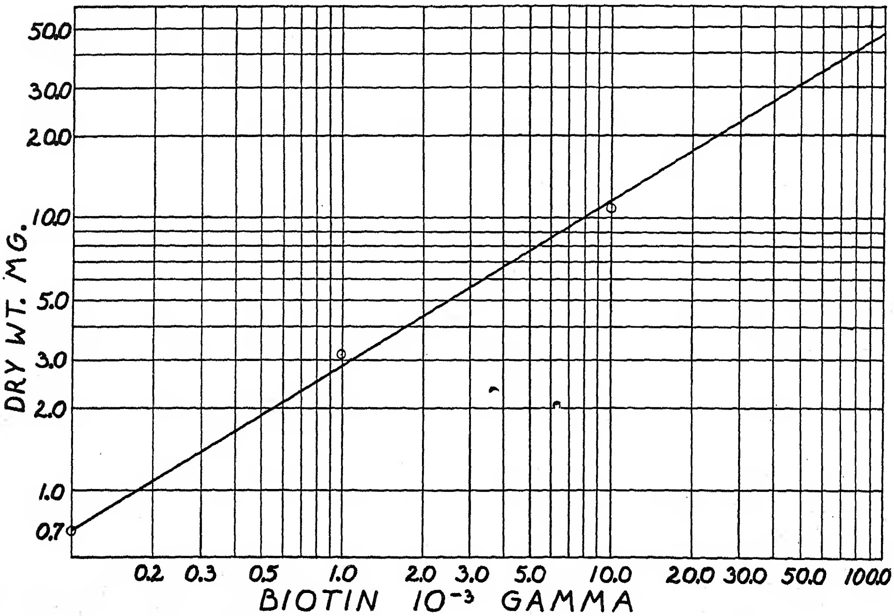

Fig. 1. Relation between logarithm of dry weight of *Ashbya gossypii* and logarithm of amount of biotin. See text for details. Data from Kögl and Fries.

Furthermore, the logarithm of the dry weight of the mycelium in mg., as given by Kögl and Fries, plotted against the logarithm of the biotin in $10^{-3}\gamma$ per flask approximates a straight line (Fig. 1). The relation between the amount of biotin per flask and mycelial growth may be expressed by the formula log biotin in $10^{-3}\gamma = 1.64$ log dry wt. mycelium in mg. -0.759. Although the data are meager we have used this curve, in lieu of more complete information, for estimating the biotin content of various substances from the dry weight of *A. gossypii* grown in their presence. We recognize that our determinations are approximations only.

Lophodermium pinastri (Schrad.) Chev., another fungus found by Kögl and Fries to require biotin, was used in some of our experiments.

EXPERIMENTAL

Methods and Materials.—The strains of *Ashbya gossypii* and *Lophodermium pinastri* employed were secured from the Centraalbureau voor Schimmelcultures, Barrn, Holland. The fungi were grown in 25 cc. of medium in 125 ml. Erlenmeyer flasks at 20–25°C. In some of the experiments the media were inoculated with a bit of the surface growth of the organism on agar slants. In other experiments a known aliquot of a spore suspension of *A. gossypii* in sterile water was added to each flask to insure uniform inoculation. The medium used in the majority of the experiments was solution B.

KH_2PO_4—0.5 g.
$MgSO_4 \cdot 7H_2O$—0.5 g.
NH_4NO_3—1.0 g.
Asparagine—5.0 g.
Cane sugar—20.0 g.
m-inositol—0.2 g.
Thiamin—0.2 mg.
Mineral supplements
Dist. H_2O—1000 cc.

The asparagine was repurified by precipitation from alcohol because we have found that the commercial product as shown by its effect upon the growth of *A. gossypii* contains some biotin or a substitute therefor. The cane sugar was Pfanstiehl sucrose C.P., *lot 409*. The mineral supplements included boron 0.01 ppm., molybdenum 0.02 ppm., iron (as ferric sulfate) 0.20 ppm., zinc 0.18 ppm., copper 0.04 ppm. and managanese 0.02 ppm. Solutions were sterilized at 15 lbs. pressure in an autoclave. Dry weights were determined by filtering the mycelium into a Gooch crucible and drying at 100°C.

A Suitable Nutrient Medium.—The maximum yield of *A. gossypii* reported by Kögl and Fries was about 12 mg. dry weight of mycelium. It seemed desirable to find a nutrient solution which would permit greater growth than they secured. A preliminary test demonstrated that a sample of light brown sugar contained biotin. To a solution of 0.5 g. KH_2PO_4, 0.5 g. $MgSO_4$. $7H_2O$, 1.0 g. of NH_4NO_3 and 20 g. of brown sugar per liter various supplements were added as follows: thiamin, 0.2 mg.; asparagine, 5 g.; inositol, 0.2 g. From 45 to 50 mg. dry weight of mycelium of *A. gossypii* were obtained (Table II) after 20 days growth in those solutions

containing asparagine. Although the addition of thiamin and inositol to the solution containing asparagine and light brown sugar had little effect on the growth of *A. gossypii* in this medium, both were used in preparing solution B in order that it might be used for *L. pinastri* also.

TABLE II

Dry weight of mycelium of A. gossypii and L. pinastri in a medium of mineral salts and 2 per cent brown sugar supplemented as indicated. Temp. 25°C., period of growth 20 days.

ADDITION	DRY WEIGHT OF MYCELIUM, MG.	
	A. gossypii	*L. pinastri*
None	7.5	9.0
Thiamin	9.5	52.0
Inositol	15.3	—
Thiamin and inositol	10.3	—
Asparagine	45.5	6.7
Asparagine and thiamin	47.0	44.5
Asparagine and inositol	50.0	—
Asparagine, inositol and thiamin	45.5	—

Buston, Kasinathan and Wylie (1938) found asparagine or ammonium aspartate satisfactory sources of nitrogen for *A. gossypii* though ammonium salts of inorganic acids and most organic acids were not adequate. It is probable that the smaller maximum yields secured by Kögl and Fries were because of the NH_4NO_3 and ammonium tartrate used as sources of nitrogen in their medium.

L. pinastri on the other hand is apparently able to utilize ammonium nitrate effectively and the addition of asparagine to the medium had no beneficial effect (Table II). Furthermore, as found by Kögl and Fries, the addition of thiamin which had little or no effect on *A. gossypii* markedly benefited the growth of *L. pinastri.*

Biotin Content of Light Brown Sugar and Molasses.—A sample of Coronet New Orleans pure molasses and one of Jack Frost light brown sugar (No. 6) were secured. Solution B was prepared with 2 per cent (on a dry weight basis) molasses instead of cane sugar. Dilutions of this stock solution were made with solution B containing pure cane sugar so that media containing 0.2 per cent, 0.02 per cent and 0.002 per cent molasses were prepared; in each of these the total sugar concentration was maintained at 2 per cent. Cultures in quintuplicate were inoculated with bits of mycelium and the cultures incubated at 20–25°C. for 20 days. A similar procedure was followed with the light brown sugar. The results are given in Table III.

TABLE III

Dry weight of A. gossypii, above, and L. pinastri, below, grown 20 days in 25 ml. of solution B with various amounts of light brown sugar or molasses. The total concentration of sugar was maintained at 2 per cent by suitable additions of pure cane sugar

PERCENTAGE IMPURE SUGAR	DRY WEIGHT OF MYCELIUM, MG.			
	2	0.2	0.02	0.002
Light brown sugar	31.9	14.6	5.5	6.6
Molasses	65.6	60.7	18.0	8.4
Check (pure cane sugar)	5.3	—	—	—
Light brown sugar	64.2	16.2	1.6	1.6
Molasses	88.8	48.6	7.4	1.0
Check (pure cane sugar)	0.8	—	—	—

In solution B with pure cane sugar (check) the yield of mycelium of *A. gosspyii* was 5.3 mg. per flask. When light brown sugar was substituted for pure cane sugar the yield was 31.9 mg. When the proportion of brown sugar was 0.2 per cent and of pure sugar 1.8 per cent the yield was reduced to 14.6 mg. Further reductions in the percentage of brown sugar resulted in further decreases in growth. The growth in the solutions containing molasses was greater than that in those containing equal amounts of the brown sugar. This was taken to mean a higher biotin content in the molasses than in the light brown sugar.

The growth of *A. gossypii* in solution B containing pure cane sugar (5.3 mg.) was many times the 0.2 mg. found by Kögl and Fries in their check solution. We believe that the growth in our check solution was due to the biotin carried in the inoculum and not because the pure cane sugar or other constituents of solution B contained biotin. This conclusion was drawn from experiments in which the amount of inoculum was varied by diluting a spore suspension with sterile water and using the same volume of the various spore dilutions for inoculum.

The effect of quantity of inoculum is shown by the following experiment: Triplicate flasks of solution B were inoculated with one drop of a spore suspension. The spore suspension was diluted 10 times and 3 flasks inoculated with 1 drop of the diluted suspension. The same procedure was followed with a dilution of 0.01 and 0.001. All cultures were grown 15 days at 23–25°C. At the 0.01 dilution approximately 40 colonies developed in each flask. The dry weight of the mycelium produced at dilution 1 was 6.4 mg. per flask; at dilution 0.1, 3.3 mg.; at 0.01, 0.2 mg. and at 0.001, 0.1 mg. Had solution B contained sufficient biotin to form 5.3 mg. of mycelium we should expect approximately the same dry weight at the various spore

dilutions. We conclude, therefore, that the growth in solution B with pure cane sugar was the result of the inoculum and differences in the yields in the check solutions of various experiments was because different quantities of inoculum were used in the various experiments.

The estimation of the biotin content of molasses and of the light brown sugar was made as follows: The growth in 2 per cent light brown sugar less that in the check solution was 26.6 mg. which is equivalent to $36\times10^{-3}\gamma$ of biotin per flask as estimated from the curve in Fig. 1. At 0.2 per cent brown sugar the net growth was 9.3 mg. which is equivalent to $6.6\times10^{-3}\gamma$ of biotin. A similar procedure was followed in estimating the biotin content in 0.02 per cent brown sugar and the various concentrations of molasses, omitting those yields which differed from the check by less than one milligram and those at the higher concentrations (2 per cent molasses) where marked inhibition of growth began to appear. The amounts of biotin per flask are given in Table VI. It is clear that in these preliminary experiments the accuracy of determination of amount of biotin is not great since the biotin per flask at 0.2 per cent should be 0.1 of that at 2 per cent and so on. Discrepancies are evident.

TABLE IV

Dry weight in mg. of A. gossypii after 15 days in solution B containing various amounts of impure sugar. The total concentration of sugar was maintained at 2 per cent by suitable additions of pure cane sugar

PERCENTAGE IMPURE SUGAR	DRY WEIGHT OF MYCELIUM MG.			
	2	0.2	0.02	0.002
Unfiltered sugar	0.2	23.6	12.8	8.2
Press filtered sugar	27.7	13.5	9.3	7.7
Washed remelt sugar	14.0	9.5	7.6	7.0
Check (pure cane sugar)	7.0	—	—	—

The response of *L. pinastri* to the light brown sugar was similar to that of *A. gossypii*. Greater growth occurred in the molasses than in the brown sugar and with dilution of the impure sugars the growth decreased.

Biotin Content of other Sugar Samples.—Since molasses appeared to have more biotin per unit of material than brown sugar, we wished to test other sugars of different purities. Through the courtesy of the American Sugar Refining Company samples of crude unfiltered refinery syrup, press filtered sugar syrup, and washed remelt sugar were obtained. The press filtered sugar syrup was darker in color than the Jack Frost light brown sugar and the washed remelt sugar was lighter in color. Solution B containing 2 per cent on a dry weight basis of each of these samples was

prepared and diluted with solution B containing 2 per cent pure cane sugar. The experiment was conducted in triplicate. The growth in pure cane sugar (Table IV) amounted to 7.0 mg. The unfiltered syrup gave the greatest yield though at 2 per cent concentration growth was inhibited probably because of salt concentration. The amount of biotin per flask was estimated as before from the curve in Fig. 1 and the results are given in Table VI.

Biotin Content of Miscellaneous Materials.—In addition to the determinations of biotin in different sugar samples, some were made of various materials as follows: Clay's fertilizer, a patent fertilizer made in London, England; egg yolk, coagulated, Bacto from the Difco laboratories; cerophyl, a dry powdered preparation of cereal grasses prepared by the American Dairies Incorporated of Kansas City, Mo.; malt flour made by crushing malt in a press under about 12,000 lbs. pressure and collecting the flour which could be rubbed through a fine sieve; peat, a partially decomposed sphagnum peat used in mulching; liquid manure, prepared by leaching cow manure.

In each instance, except for the liquid manure, 2 per cent of the material was boiled for ½ hour in solution B without sugar and filtered through Whatman No. 50 and No. 42 filter paper. To the filtrate 2 per cent pure cane sugar was added and the solution diluted with solution B containing 2 per cent cane sugar to obtain various concentrations. To the liquid manure which contained 0.34 per cent dry matter 2 per cent cane sugar was added and the solution diluted with solution B containing 2 per cent cane sugar. The experiment was run in triplicate for 15 days.

TABLE V

Dry weight of mycelium of A. gossypii grown 15 days in solution B plus various quantities of the substances given. All solutions contained 2 per cent pure cane sugar

PERCENTAGE SUBSTANCE	DRY WEIGHT OF MYCELIUM, MG.			
	2	0.2	0.02	0.002
Clay's fertilizer	22.1	13.5	7.3	5.7
Egg yolk	no growth	19.7	10.8	5.8
Cerophyl	46.6	27.2	11.3	6.4
Malt flour	39.3	14.2	4.9	5.0
Peat	9.2	5.7	5.7	5.0
Liquid manure	—	no growth	28.3	10.2
Check (pure cane sugar)	5.3	—	—	—

The growth in solution B containing pure cane sugar (check) amounted to 5.3 mg. (Table V). The egg yolk at the highest concentration and the

liquid manure at 0.2 per cent inhibited growth. The amounts of biotin per flask estimated from the dry weight by means of the curve in Fig. 1 are given in Table VI.

TABLE VI

Biotin content in 10^{-3} γ per flask at various dilutions of substances given

PERCENTAGE SUBSTANCE	AMOUNT OF BIOTIN PER FLASK 10^{-3} GAMMA			
	2.0	0.2	0.02	0.002
Light brown sugar	36.0	6.6	0.24	—
Molasses	—	11.0	1.1	0.22
Unfiltered sugar	—	16.5	3.0	—
Press filtered sugar	23.5	3.7	0.7	—
Washed remelt sugar	4.2	0.78	—	—
Clay's fertilizer	17.0	5.5	0.55	—
Egg yolk (dried)	—	13.0	2.8	—
Cerophyl	72.0	26.0	3.2	0.21
Malt flour	53.0	6.0	—	—
Peat	1.6	—	—	—
Liquid manure	—	—	28.0	2.3

Biotin Content per gram.—From the data in Table VI we have calculated the amount of biotin per gram dry weight of the various materials used (Table VII). In general, we regard the amounts determined at the lower concentrations as more accurate because in many instances at the higher concentrations toxicity inhibits growth to a greater or less extent. It may be possible also that the curve in Fig. 1 is not accurate for the larger amounts of biotin.

TABLE VII

Amount of biotin in 10^{-3} γ per g. in various substances tested

	BIOTIN PER G. 10^{-3} GAMMA
Unfiltered syrup	600
Molasses	220
Press filtered sugar	107
Light brown sugar	60
Washed remelt sugar	11
Clay's fertilizer	110
Egg yolk	560
Egg yolk (Kögl)	530
Cerophyl	585
Malt flour	118
Peat	3
Liquid manure (per ml.)	5,100
Liquid manure (per g. dry matter)	150,000

For example, the 50 mg. of unfiltered syrup in each flask at the 0.2 per cent concentration contained $16.5\times10^{-3}\gamma$ of biotin or $320\times10^{-3}\gamma$ per g. On the basis of the determination made at the 0.02 per cent concentration the figure would be $600\times10^{-3}\gamma$ per flask. We have used the latter figure (Table VII) and eliminated the former because of the inhibition of growth at higher concentrations of the unfiltered syrup. Molasses at both 0.2 and 0.02 per cent (Table VI) gives us $220\times10^{-3}\gamma$ of biotin per gram. For 0.2 per cent light brown sugar we believe the amount of biotin per flask as determined is too high and in estimating the biotin per gram of light brown sugar have averaged the values obtained at 0.02 and 2 per cent concentrations. For the press filtered sugar syrup we have averaged the values calculated from the amounts of biotin at 0.02 and 0.2 per cent; and for the washed remelt sugar we have taken an average of the values calculated from the amounts of biotin at 0.2 and 2 per cent. The biotin per g. of Clay's fertilizer is the same, $110\times10^{-3}\gamma$, as determined at 0.02 and 0.2 per cent. For egg yolk we considered as more reliable the biotin content estimated from the results secured at 0.02 per cent. The biotin content of cerophyl per g. was obtained by averaging the figures calculated from the biotin per flask at 0.02 and 0.2 per cent; and for malt flour an average was taken of the values obtained at 0.2 and 2 per cent.

Extraction of Biotin from Molasses.—An attempt was made to concentrate biotin from molasses. The molasses was neutralized with $Ba(OH)_2$ and extracted with methl alcohol which was removed under reduced pressure. The residue from the methyl alcohol extract was taken up in water and treated with CO_2 to remove the barium. The solution was then treated with "decalso" which had been previously extracted with acetic acid, HCl and KCl. The "decalso" was extracted with ammoniacal acetone, the extract evaporated to dryness and taken up in 80 per cent ethyl alcohol. The alcohol was evaporated and the residue dissolved in water.

The extract prepared as above was added to solution B containing pure cane sugar in amounts equivalent to 50 per cent, 10 per cent, 2 per cent and 0.4 per cent molasses. The dry matter added per flask for each of these concentrations was 34.0 mg., 6.8 mg., 1.35 mg. and 0.27 mg. respectively. The cultures were grown in triplicate at 25°C. for 15 days. The dry weights are given in Table VIII. From the net dry weights the biotin content per flask was estimated by using the curve in Fig. 1. For the lower concentrations the amount of biotin per flask agrees well with the dilutions. In the last column of Table VIII we have given the biotin content per g. of dry matter in the extract.

By the extraction the biotin per g. of dry matter was concentrated

TABLE VIII

Dry weights of mycelium of A. gossypii grown in solution B plus various amounts of an extract of molasses and the amount of biotin calculated from the growth

EXTRACT EQUIVALENT TO MOLASSES OF	DRY WEIGHT MYCELIUM, MG.	NET DRY WEIGHT, MG.	BIOTIN PER FLASK, 10^{-3} GAMMA	BIOTIN PER G. 10^{-3} GAMMA
50 per cent	50.0	37.2	60.0	1620
10 per cent	31.9	19.1	21.5	3200
2 per cent	18.6	5.8	3.0	2200
0.4 per cent	14.9	2.1	0.6	2200
Check	12.8	—	—	—

about ten times, an unsatisfactory result. However, the figures are of interest because they indicate that the method of determining biotin is of some reliability.

Substitutes for Biotin.—A sample of 50 per cent calcium pantothenate supplied by Dr. R. J. Williams, was used in solution B with 2 per cent cerelose at 0.5, 0.05, 0.005, 0.0005, 0.00005 and 0.000005 mg. per flask. No effect was observed on the growth of *A. gossypii.* A less pure sample, pantothenic acid concentrate, Ca salts, No. 133, gave some increase in growth at 5 mg. per flask. We conclude that biotin and pantothenic acid are not identical though impure samples of the latter may contain some biotin.

Pure crystalline B_6, supplied through the courtesy of Merck and Co., was added in amount of 10γ, 1γ, 0.1γ or 0.01γ per flask of solution B. No effect on the growth of either *A. gossypii* or *L. pinastri* was observed. We conclude that biotin and B_6 are not identical.

DISCUSSION

The results of these preliminary experiments are not presented as definitive findings but as suggestive ones only. Before much reliability can be placed on the use of *A. gossypii* for the quantitative estimation of biotin further studies should be made of the relation between the dry weight of the organism and amount of biotin under various conditions (media, temperature, etc.). However, the quantity of biotin we found in dried egg yolk agrees fairly well with that found by Kögl and Tönnis using yeast growth as a means of estimating biotin content. Furthermore, the results with various sugars are of the order which might be anticipated, the amount of biotin per g. decreases as the sugar is purified. The purity of the sugar samples may be roughly estimated from their ash contents. On a dry weight basis they were as follows: Unfiltered syrup, 8.9 per cent; Coronet molasses, 8.25 per cent; press filtered washed syrup, 3.08 per cent; light brown

sugar No. 6, 0.92 per cent; light brown sugar No. 5, 0.84 per cent and washed remelt sugar, 0.075 per cent. The biotin contents of these various sugars are not directly proportional to their ash contents, but the arrangement of the sugars in the order of their biotin contents and of their ash contents is the same.

Kögl and Tönnis used the growth of a strain of yeast for estimating biotin, and their method is preferable to the use of *A. gossypii*, because the time necessary for a determination with yeast is but 5 hours. When time is not a factor the growth of *Ashbya* might be employed and perhaps under certain circumstances might be a better means than yeast. In our experiments, *L. pinastri* was not as sensitive as *A. gossypii* to the more minute quantities of biotin.

Of the substances investigated, liquid manure contained the largest amount of biotin per g. dry matter. Whether the biotin was derived entirely from the manure which was leached or in part from bacterial growth while the liquid manure stood in the pit remains to be determined. In any event, liquid manure would seem to be a better source of biotin than dried egg yolk from which Kögl and Tönnis originally isolated it. It is probable that the evaporated juice of the sugar cane from which the first crystallization of sugar is made is richer in biotin than dried egg yolk. The unfiltered syrup, cerophyl and dried egg yolk were about equally rich in biotin and superior to the other substances investigated. Since the biotin is removed in the purification of the sugar, it is probable that the original evaporated sugar cane juice would show a still higher biotin content than that found in any of the sugar samples investigated, and the bone black used in sugar refining might contain considerable adsorbed biotin and prove a superior source for that growth substance.

It is possible that, like thiamin, biotin is a growth substance needed by all or almost all organisms and like thiamin some of them are able to construct it from more elementary materials while others, lacking that ability, require an external supply. Aside from a few fungi which have been demonstrated to need for growth an external supply of biotin and strains of yeast with which Kögl has worked little is known of the biotin requirements of living organisms. Kögl and Haagen Smit (1936) reported that biotin increases the growth in length of pea seedlings from which cotyledons have been removed. Kögl, Thimann and Went, see Went and Thimann (1937), found that biotin increases the roots on etiolated pea stems. Progress in our knowledge of the importance of biotin as a growth substance and of its function will be delayed until adequate quantities of pure biotin are available.

SUMMARY

A means of estimating amounts of biotin from the growth of *Ashbya gossypii* based on data from Kögl and Fries is described.

The amount of biotin in a sample of liquid manure was found to be $150{,}000 \times 10^{-3}$ γ per g. of dry weight, unfiltered syrup, cerophyl and egg yolk contained about 600 units and other substances tested smaller quantities.

The amount of biotin decreased with the purity of the sugar samples tested.

Neither pantothenic acid nor vitamin B_6 were found to replace biotin.

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Oligocene Island Fungi

William A. Murrill

Since I have been spending my summers in Florida a new mycological world has been opened up to me, with many strange and wonderful forms never heard of, nor even dreamed of, before. As I write these lines I note on a blotter beside me that three hundred and twelve new species have been described from this region during the past year. Why are they here in the first place; and why have they been overlooked for so long? I believe I have the answer to both of these questions.

The "Oligocene Island" extends from near the south bank of the Suwannee River to the south end of St. Petersburg Bay; and Alachua County, the special field of my recent explorations, lies well within its boundaries. All this region was once a real island and retained its insular character continuously over a period of at least twelve million years before being connected with the mainland. Its early climate being tropical, its original species were naturally those of adjacent lands in tropical America, while its insular character favored the development of many new species from the original ones.

These endemic species, being produced in a warm climate, naturally prefer summer to winter, especially since the Florida summer is also the season of frequent rains. But American mycologists have had a different preference, shunning Florida during the summer months and thus allowing these wonderful endemic species to rot where they grew. It has just been my good fortune to see them first; that is all.

A different story, which does not interest me at the moment, would deal with the migration of species from the Oligocene Island both southward and northward when conditions became favorable and the introduction of northern species during successive periods of glaciation in the Pleistocene, the whole making a tale so complicated, so fascinating, as to be almost unbelievable.

A few selected tropical species found in Alachua County will serve for illustration. Many of these are widely distributed in tropical America and some have made their way into the warmer parts of the United States.

Armillaria alphitophylla
Armillaria Boryana
Lentinus crinitus
Lepiota Morgani
Plicatura lateritia
Stereum elegans
Stereum lobatum
Coriolopsis crocata
Coriolus pinsitus
Coriolus sector
Cycloporellus iodinus
Earliella corrugata
Elfvingia tornata
Gloeophyllum striatum
Hapalopilus licnoides
Hexagona daedalea
Microporellus mutabilis
Nigroporus vinosus
Pogonomyces hydnoides
Poria vincta
Pycnoporus sanguineus
Rigidoporus surinamensis

Some rather peculiar things have happened in connection with the migration of these tropical species to the Oligocene Island. *Inonotus fruticum*, for example, described from specimens growing on shrubs in Cuba, is found here only on the dwarf papaws, often in abundance. Another example of specialization in host is *Coriolus membranaceus taxodii*, found here only on cypress, the typical form of the species being absent. *Fomes geotropus*, coming up from the West Indies, seems to have continued its normal life on hardwoods and also developed a special race on cypress. *Polyporus virgatus*, from Cuba, expanded into quite a different thing as *P. Rhoadsii;* while *Hirneola Wrightii*, known only from Alachua County and Cuba, may have originated in either place and migrated to the other.

But the development of endemic species in the long period of quiet on Oligocene Island has interested me most during the past few years. To illustrate, I will use four genera of fleshy fungi, *Boletus*, *Agaricus*, *Russula*, and *Amanita*. In the first the northern species commonly seen are *B. edulis*, *B. communis*, *B. bicolor*, *B. granulatus*, *B. luridus*, *B. felleus*, and *B. strobilaceus;* while several others are rare or frequent. But when one wants a fine mess for a party he goes for *B. aureissimus;* for size he seeks out *B. pisciodorus;* and for beauty *B. ananas*, *B. hemichrysus*, *B. subflavidus*, or *B. pictiformis*. These are strange names to the northerner; as the boletes are strangers to the tropics.

In *Agaricus* the chief pasture species is *A. projectellus*, the woodland species *A. pocillator*, the sand-loving species *A. floridanus*, and the lover of cultivated land *A. auricolor*. Even *A. placomyces* is represented by its var. *badius;* while the only northern species commonly seen is *A. sylvicola*. This genus resembles *Boletus* in its aversion to a strictly tropical climate.

In *Russula* there is a lavish display of endemic species. As in the case of the chemical elements, one can select his requirements in advance and always find a species to fit them—sometimes three or four! The lovers of the lawns are *R. subalbidula*, *R. subochrophylla*, and *R. uncialiformis*, as well as the well-known temperate species, *R. pectinatoides*. In the woods one finds *R. Mariae*, *R. crustosa*, and *R. variata*, but more abundant than all these is *R. heterospora*, that species with the remarkable spores discovered by Beardslee. I have no doubt that it originated right here on Oligocene Island.

And the same holds good, I am sure, for many local species of *Amanita*. Among the common temperate species might be listed *A. flavoconia*, *A. gemmata*, *A. phalloides*, *A. verna*, and *A. flavorubescens;* but the species one encounters most frequently about the haunts of men is *A. Roanokensis*, a radical departure in the matter of spores that doubtless originated here and spread sparingly northward as far as North Carolina, where Coker

discovered it. There are also several other species here, close relatives of *A. Roanokensis*, with cylindric spores.

The genus *Amanita* as represented in Alachua County affords one of the best opportunities I know to study and use odors in the differentiation of species. Unfortunately, some persons are odor-blind just as others are color-blind but I have no complaint to make; as my *A. anisata*, *A. suballiacea*, *A. virosiformis*, *A. alliacea*, and *A. odorifera* will indicate. There are odors of the kitchen, of boiling beef, of anise, of chloride of lime, of wild onion, of skunk, of carrion, and of ground bone mixed with caramel. The last-mentioned combination persisted for months in the herbarium after the mummified remains of *A. odorifera* were neatly laid away.

Perhaps I have said enough to show that I am enjoying the delights and responsibilities of a region quite novel and exceedingly interesting mycologically.

Numbers cited in describing the following new species refer to collections in the herbarium of the Florida Agricultural Experiment Station, at Gainesville.

Lepiota praegraveolens sp. nov. Pileo convexo-depresso, 6–8 cm. lato, glabro, albo; sporis globosis, 10μ; stipite albo, 10×1 cm.; annulo albo.

Pileus convex to deeply depressed, gregarious, 6–8 cm. broad; surface smooth, glabrous, white, unchanging, margin inflexed, widely sterile, appendiculate; context thin, white, unchanging, taste decided but not specially unpleasant, odor very strong and disagreeable, earthy mixed with something worse; lamellae free to remote, tapering behind, narrow, crowded, inserted, white, unchanging, edges thin, uneven and much eroded; spores globose, apiculate, finely roughened, granular, hyaline, about 10μ; cystidia none; stipe long, solid, equal above the onion-shaped bulb, beautifully longitudinally grooved, subglabrous, white, unchanging, about 10×1 cm.; annulus near the apex, white, membranous, fixed, clinging like a ragged, wet skirt.

Type collected by W. A. Murrill in open, grassy soil near a stable in Gainesville, Fla., Oct. 25, 1938 (*F 18298*). A remarkable species, probably nearest to *L. naucina*, but unattractive to the mycophagist because of its disagreeable odor. The surface of the sphores is distinctly roughened.

Lepiota rubriceps sp. nov. Pileo convexo-plano, umbonato, 1 cm. lato, rubro; lamellis ochroleucis; sporis $6\times 4\mu$; stipite 1.5 cm. longo; annulo subflavo, rubro-marginato.

Pileus convex to plane with a conspicuous rounded umbo, solitary, 1 cm. broad; surface smooth, minutely tomentose under a lens, uniformly ruber, margin even, entire; context very thin, white, unchanging; lamellae free, rounded behind, ventricose, inserted, rather broad, crowded, entire, ochroleucous; spores elongate-ovoid, smooth, hyaline, obliquely apiculate, 1-guttulate, about $6\times 4\mu$; cystidia none; stipe equal, smooth, glabrous above the ring,

slightly viscid and stramineous below, 1.5×0.15 cm.; annulus fixed, median, membranous, small, pale-yellow, the margin red and pointing upward.

Type collected by West and Murrill on the ground under hardwood trees in South Planera Hammock, eleven miles northwest of Gainesville, Fla., Oct. 26, 1938 (*F 18307*). Very pretty and dainty, with short, white stem, yellow gills and red cap.

Lepiota subcristatella sp. nov. Pileo convexo-plano, 1.5 cm. lato, albo, fibrilloso; sporis ellipsoideis, 6–7×3–4μ; stipite subviscido, clavato, rosei-avellaneo, 3×0.05–0.1 cm.; annulo albo.

Pileus convex to plane, becoming umbonate when dried, solitary, about 1.5 cm. broad; surface dry, pure-white, fibrillose, glabrous on the isabelline disk, becoming striate when dried; context very thin, white, unchanging; lamellae free, inserted, medium broad, medium distant, finely fimbriate, white, unchanging; spores ellipsoid or ovoid, smooth, hyaline, obliquely apiculate, 1-guttulate, 6–7×3–4μ; stipe tapering upward from a clavate base, slightly viscid, minutely pruinose, pallid to rosy-avellaneous, about 3 cm. long and 0.5–1 mm. thick; annulus fixed below the middle, white, membranous, persistent.

Type collected by West, Arnold and Murrill on the ground under hardwood trees in Planera Hammock, eleven miles northwest of Gainesville, Fla., Oct. 21, 1938 (*F 18305*). Also collected by the same persons at Sugarfoot, Oct. 18, 1938 (*F 18293*). Found sparingly in the autumn under hardwood trees, usually solitary, looking very white and neat.

Lepiota subdryophila sp. nov. Pileo convexo, umbonato, 4 cm. lato, albo, umbrino-squamuloso; sporis 9–10×7–8μ; stipite albo, glabro, 6×0.4 cm.; annulo amplo, albo et rubro-brunneo.

Pileus broadly convex with a broad umbo, gregarious, about 4 cm. broad; surface dry, white, with umbrinous umbo and umbrinous, small, pointed scales; context thin, white, unchanging; lamellae free, close, medium broad, inserted, entire, white, with a faint pink tint when dried; spores broadly ellipsoid or ovoid, smooth, hyaline, obliquely apiculate, 1-guttulate, 9–10×7–8μ; cystidia none; stipe bulbous, smooth, glabrous, white, dark-gray in dried specimens, about 6×0.4 cm.; annulus 2 cm. from the apex, ample, fixed, membranous, white, reddish-brown below.

Type collected by West, Arnold and Murrill on a rotten hardwood log in Planera Hammock, eleven miles northwest of Gainesville, Fla., Oct. 21, 1938 (*F 18297*). Near *L. dryophila* Murrill, found on an oak log in New Orleans, but having a much slenderer stipe. The dried specimens are very pretty with their tiny scales and the faint blush on their gills.

Russula albiflavescens sp. nov. Pileo convexo-subdepresso, 4 cm. lato, albo, striato, sapore grato; sporis ochroleucis, tuberculatis, 8×6μ; stipite albo, clavato, 5×0.7–1 cm.

Pileus convex to slightly depressed, solitary, 4 cm. broad; surface slightly viscid, glabrous, milk-white, slightly yellowish when dry, margin sulcate-striate; context thin, white, unchanging, odorless, mild; lamellae adnate, equal, a few forked at the base, medium broad, medium distant, entire, pallid to ochroleucous; spores broadly ellipsoid, strongly tuberculate, apiculate, ochroleucous in mass, about 8×6μ; cystidia none; stipe tapering upward from a clavate base, slightly enlarged at the apex, smooth, glabrous, white, unchanging, 5×0.7–1 cm.

Type collected by W. A. Murrill in soil under *Pittosporum* in Gainesville, Fla., Oct. 25, 1938 (*F 18294*). Pure-white with decidedly yellow spores and very light in weight when dried. Probably nearest to *R. Westii* Murrill but entirely distinct from it.

Russula pinetorum sp. nov. Pileo convexo-depresso, 6 cm. lato, roseo-isabellino, acrido; lamellis adnatis, albis, sporis albis, 8–10×6–8μ; stipite subpallido, 5×1 cm.

Pileus convex to somewhat depressed, solitary, 6 cm. broad; surface slightly viscid, smooth, glabrous, varied with pallid and pale-rosy-isabelline; margin entire, slightly striate, peeling readily; context white, unchanging, odorless, very thin, soon becoming decidedly acrid and bitter; lamellae adnate, some forked at the base, practically all equal, ventricose, medium broad, rather close, entire, pure-white, unchanging; spores globose to broadly ellipsoid, distinctly echinulate, chalk-white in mass. 8–10×6–8μ; cystidia none; stipe equal, except abruptly enlarged at the apex, smooth, glabrous, very-pale-avellaneous, drying reddish-brown, about 5×1 cm.

Type collected by W. A. Murrill on the remains of a decayed pine log just east of Gainesville, Fla., Oct. 29, 1938 (*F 18315*). In the dried specimens the colors are brighter, showing purple and slightly greenish tints, while the stem is collapsed as in *Tricholoma*.

Russula subobscura sp. nov. Pileo convexo-depresso, 4–6 cm. lato, purpureo-rubro, sapore grato; sporis ochroleucis, echinulatis, 9×7μ; cystidiis 60–75×10–12μ; stipite albo, 5×1.5 cm.

Pileus convex to depressed, gregarious, 4–6 cm. broad; surface uneven, glabrous, dark-purplish-red, margin even, entire, peeling readily; context thin, odorless, mild, white, slightly gray when dried; lamellae subadnate, ventricose, medium broad, equal, some forked at the base, medium distant, entire, white to ochroleucous; spores ochroleucous in mass, broadly ellipsoid, distinctly echinulate, some 1-guttulate, about 9×7μ; cystidia abundant, resembling spear-heads, ventricose, pointed, hyaline, 60–75×10–12μ; stipe equal, smooth, glabrous, milk-white, becoming griseous or fumosous when handled or on drying, about 5×1.5 cm.

Type collected by West and Murrill on the ground under hardwood trees in South Planera Hammock, eleven miles northwest of Gainesville,

Fla, Oct. 26, 1938 (*F 18301*). Apparently rare, found only once. The cystidia are very striking, as is the change in the stem from pure-white to dark-steel-gray.

Russula subsericeonitens sp. nov. Pileo convexo-subdepresso, 5 cm. lato, atropurpureo; lamellis adnexis, albis, sporis albis, 6–8×6–7μ; stipite albo, 5×1–1.3 cm.

Pileus convex to slightly depressed, solitary, about 5 cm. broad; surface slightly viscid, smooth, subglabrous, opaque, atropurpureous, blackish on the disk, margin even, entire, peeling easily; context thin, white, unchanging, odorless, mild at first, becoming slightly acrid but eaten by squirrels; lamellae almost free, narrow and blunt behind, medium broad in front, mostly equal, none forked, medium distant, white, unchanging; spores chalk-white in mass, globose to broadly ellipsoid, distinctly echinulate, 1-guttulate, 6–8×6–7μ; cystidia none; stipe slightly tapering upward, glabrous, somewhat uneven, white, unchanging, 5×1–1.3 cm.

Type collected by W. A. Murrill in wet soil in a low hammock under pine and hardwood trees at Gainesville, Fla., Oct. 28, 1938 (*F 18310*). Much like *R. sericeonitens* but drying thinner and lighter; and having spores that vary to broadly ellipsoid, gills that do not fork and are narrower and more distant, and flesh that tastes slightly acrid after a short time.

Russula Watsoniana sp. nov. Pileo convexo-subdepresso, 8 cm. lato, roseo ad cremeo, sapore grato; lamellis adnatis, sporis ochroleucis, 10–12×6–8μ; cystidia 60×10μ; stipite subroseo, glabro, 5×1.5 cm.

Pileus convex to slightly depressed, solitary, 8 cm. broad; surface smooth, glabrous, rosy-avellaneous-isabelline with some cremeous shades, margin even, entire, peeling but slightly; context thick, firm, white, unchanging, odorless, mild; lamellae adnate, some forked at the base, equal, plane, broad, close, entire, white to ochroleucous; spores broadly ellipsoid, strongly echinulate, ochroleucous in mass, 10–12×6–8μ; cystidia like lance-heads, abundant, smooth, hyaline, ventricose, pointed, about 60×10μ; stipe equal, smooth, glabrous, solid, pale-roseous, about 5×1.5 cm.

Type collected by J. R. Watson and W. A. Murrill on the ground in mixed woods just east of Gainesville, Fla., Oct. 29, 1938 (*F 18316*). A fine, firm species, enjoyed by squirrels, having a mixture of pale colors on the cap and a pale-rosy stem. Dr. Watson is a well-known entomologist who finds many interesting insects on the fungi.

Clitocybe subpinophila sp. nov. Pileo convexo, 4–5 cm. lato, glabro, roseo-isabellino; lamellis albis, confertis, sporis ovoideis, 5×3μ; stipite albo, 4×0.4 cm.

Pileus broadly convex, solitary, 4–5 cm. broad; surface dry, smooth, glabrous, uniformly rosy-isabelline, margin paler, even, slightly lobed; context very thin, white, odorless; lamellae short-decurrent, narrow, crowded, in-

serted, entire, white, unchanging; spores broadly ovoid, tapering at one end, apiculate, smooth, hyaline, about $5 \times 3\mu$; cystidia none; stipe equal, flexuous, smooth, glabrous, white, unchanging, 4×0.4 cm.

Type collected by W. A. Murrill on the ground under hardwood trees at Gainesville, Fla., Sept. 3, 1938 (*F 18323*). A rare species, neither umbonate nor umbilicate, distantly suggesting *C. pinophila* (Peck) Sacc.

Clitocybe subtruncicola sp. nov. Pileo convexo-subdepresso, 2–3 cm. lato, albo; lamellis adnatis, sporis ovoideis, $3 \times 2\mu$; stipite albo, pruinoso, 3×0.2–0.4 cm.

Pileus convex to slightly depressed, gregarious, 2–3 cm. broad; surface dry, smooth, glabrous, milk-white, unchanging, margin even, entire; context white, mild, odorless; lamellae adnate with decurrent tooth, rather broad, inserted, close, entire, white, unchanging; spores ovoid, smooth, hyaline, about $3 \times 2\mu$; cystidia none; stipe equal or tapering upward, tough, smooth, pruinose, white, unchanging, about 3×0.2–0.4 cm.

Type collected by West, Arnold and Murrill on a rotten oak log in Planera Hammock, eleven miles northwest of Gainesville, Fla., Oct. 21, 1938 (*F 18302*). White throughout, with small, ovoid spores.

Gymnopus aurantiacus sp. nov. Pileo hemisphaerico, caespitoso, 1.5–2 cm. lato, aurantiaco ad ochraceo-ferrugineo, glabro; lamellis adnatis, albis; sporis fusoideis, 6–$8 \times 3\ \mu$; stipite glabro, albo fulvoque, 4×0.2–0.4 cm.

Pileus regularly hemispheric, cespitose, 1.5–2 cm. broad; surface smooth, glabrous, uniformly orange when young, becoming ochraceous-ferruginous or paler, margin even, entire; context membranous, tough, not reviving; lamellae adnate, arcuate, medium distant, narrow, inserted, entire, white; spores fusiform, smooth, hyaline, 6–$8 \times 3\mu$; cystidia none; stipe tapering upward, smooth, glabrous, slightly pruinose at the apex, white above, rusty to fulvous below, white-tomentose at the base, about 4×0.2–0.4 cm.

Type collected by West, Arnold and Murrill on much-decayed oak wood in Planera Hammock, eleven miles northwest of Gainesville, Fla., July 21, 1938 (*F 17904*). Also collected by West, Arnold and Murrill on a hardwood log in Planera Hammock, July 16, 1938 (*F 17803*); and by West and Murrill on an oak log in Kelley's Hammock, July 19, 1938 (*F 18281*). Densely clustered, abundant, and highly colored. It might easily go into *Marasmius* but does not revive when moistened.

Gymnopus castaneidiscus sp. nov. Pileo convexo-subexpanso, 4–8 cm. lato, castaneo vel badio, glabro; lamellis praeconfertis, sporis 7–8×3.5–4μ; stipite clavato, 4–6×0.6–1 cm.

Pileus convex to subexpanded, gregarious or cespitose, 4–8 cm. broad; surface smooth, glabrous, the cuticle often cracking radially, castaneous at the center, then bay, fading out toward the striate, lobed and rimose margin; context very thin, dull-whitish, mild, with a slight odor of sour dough; lamellae

adnexed, rounded behind, very narrow, inserted, very crowded, entire, pallid; spores oblong-ellipsoid, smooth, hyaline, obliquely apiculate, granular, 7–8 $\times 3.5$–4μ; stipe tapering upward, smooth, glabrous, pruinose or tomentose at the apex, pallid, darker at the base, hollow, clavate, 4–6 $\times$ 0.6–1 cm.

Type collected by West and Murrill on a much-decayed hickory log in South Planera Hammock, eleven miles northwest of Gainesville, Fla., Oct. 26, 1938 (*F 18312*). Also collected frequently during the summer on hardwood logs about Gainesville (*F 18300*, *F 18308*, *F 18313*, *F 17471*, *F 17891*). Suggesting *G. acervatus* (Fries) Murrill but with longer spores and paler, much thicker stipe. Near *G. subluxurians* Murrill but growing on wood, darker in color, and having more slender spores.

Gymnopus floridanus sp. nov. Pileo convexo, 5–10 mm. lato, striato, pruinoso, glauco-plumbeo; lamellis adnatis, caesiis; stipite hyalino, 1.5–2 $\times$ 0.2 cm.

Pileus convex to slightly depressed with a fluffy, whitish, conic or irregular papilla, gregarious to cespitose, about 5–7 mm. broad, rarely reaching 1 cm.; surface moist, not viscid, finely striate, pruinose or finely fibrillose, glauco-plumbeous; margin entire, deflexed, pallid on the extreme edge; context membranous, tough, pallid, odorless, mild; lamellae squarely adnate, inserted, narrow, distant, entire, caesious with a caeruleous tint; cystidia none; spores not found; stipe smooth, pruinose, hyaline, enlarged and white-tomentose at the base, about 1.5–2 $\times$ 0.2 cm.

Type collected by West and Murrill on a much-decayed sweet-gum log in Kelley's Hammock, ten miles northwest of Gainesville, Fla., Aug. 3, 1938 (*F 18290*). Very abundant on this one log but not seen elsewhere. Peculiar both in form and color. Tough enough for *Marasmius* but not reviving in proper fashion under treatment.

Gymnopus mammillatus sp. nov. Pileo convexo-subexpanso, 2–3 cm. lato, albo, umbonato, sporis ellipsoideis, $8 \times 3\mu$; stipite glabro, albo, 3–5 $\times$ 0.3–0.5 cm.

Pileus convex to subexpanded, gregarious, about 2–3 cm. broad; surface smooth, glabrous, shining, white, pale-isabelline on the conspicuous umbo, margin even, entire to slightly striate; context thin, odorless, mild, white, unchanging; lamellae just touching the stipe, becoming remote, rounded behind, narrow, crowded, inserted, white, unchanging, the edges finely notched; spores oblong-ellipsoid, smooth, hyaline, granular, obliquely apiculate, $8 \times 3\mu$; cystidia none; stipe tapering upward from an ovoid bulb, smooth, glabrous, white, much twisted at times and light-reddish-brown when dried, 3–5 $\times$ 0.3–0.5 cm., the bulb 1 cm. thick.

Type collected by W. A. Murrill in wet soil under bamboos at Gainesville, Fla., Oct. 28, 1938 (*F 18319*). Also collected by W. A. Murrill on the ground in a high hammock at Gainesville, Fla., Oct. 17, 1938 (*F 18306*). Suggesting *G. albistrictus* Murrill, but gregarious and umbonate.

Hydrocybe nitida lutea var. nov. Pileo convexo, 1–2 cm. lato, viscido, luteo, sulcato.

Pileus convex or slightly depressed, usually papillate, gregarious, 1–2 cm. broad; surface moderately viscid, uniformly luteous, glabrous, margin entire, sulcate; lamellae arcuate, broad behind, distant, decurrent, inserted, entire, yellow; spores ellipsoid or ovoid, smooth, hyaline, granular, $6–8 \times 4–5 \mu$; cystidia none; stipe usually slightly tapering downward, viscid, smooth, concolorous, glabrous, $3–6 \times 0.2–0.3$ cm.

Type collected by W. A. Murrill among moss in wet ground in Planera Hammock, eleven miles northwest of Gainesville, Fla., Aug. 13, 1938 (*F 18291*). Also collected by West and Murrill in Planera Hammock, July 20, 1938 (*F 18046*). Agreeing fairly well with *H. nitida* (Berk. & Curt.) Murrill, described from South Carolina, but egg-yellow instead of pale-yellow and hardly umbilicate.

Hydrocybe subruber sp. nov. Pileo conico, 3–5 cm. lato, viscido, luteo ad flavo; lamellis citrinis; sporis $10–12 \times 5 \mu$; stipite subluteo et albo, $6–8 \times 0.7$ cm.

Pileus conic with conic umbo, gregarious, 3–5 cm. broad; surface viscid, glabrous, uniformly luteous when young, becoming flavous except at the center, margin becoming striate, rimose and much upturned in age; context very thin, subluteous, odorless, mild; lamellae adnexed, ventricose, broad, inserted, citrinous, edges becoming very uneven, fragile and rimose; spores oblong-ellipsoid, smooth, hyaline, granular, $10–12 \times 5 \mu$; cystidia none; stipe equal, smooth, glabrous, viscid, subluteous, white at the base, $6–8 \times 0.7$ cm.

Type collected by West and Murrill on the ground under hardwood trees in South Planera Hammock, eleven miles northwest of Gainesville, Fla., Oct. 26, 1938 (*F 18299*). Fairly frequent in hammocks about Gainesville after warm rains. Very striking because of its shape and color. *H. ruber* Peck is red and has smaller spores.

Hygrophorus subluridus sp. nov. Pileo convexo-expanso, umbonato, 3 cm. lato, viscido, fusco; lamellis confertis, sporis globosis, $3–4 \mu$; stipite glabro, subfusco, 6×0.4 cm.

Pileus convex to expanded, broadly umbonate, solitary, about 3 cm. broad; surface slimy-viscid, fuscous, glabrous, delicately reticulate in part, margin even, entire; context rather thin, white, unchanging, odorless; lamellae adnexed, rounded behind, ventricose, crowded, inserted, entire, pallid to fuscous; spores globose or subglobose, smooth, hyaline, $3–4 \mu$; cystidia none; stipe equal, smooth, glabrous, subconcolorous, about 6×0.4 cm.

Type collected by Rhoads and Murrill on the ground under an oak at Hunter's Station, near Gainesville, Fla., Sept. 6, 1938 (*F 18292*). Suggesting *H. subpratensis* Murrill, a Cuban species, but the gills are not sinuate and the pileus does not fade. In *H. floridanus* Murrill the gills are distant.

Marasmius domesticus sp. nov. Pileo convexo-plano, 2–3 cm. lato, isabellino; lamellis adnatis, avellaneis; sporis ellipsoideis, 6×4 μ; stipite avellaneo, $3–4 \times 0.2–0.3$ cm.

Pileus convex to plane or slightly depressed, often with a small umbo, gregarious to subcespitose, 2–3 cm. broad; surface glabrous, more or less striate and uneven, dark-isabelline when fresh and moist, paler when dry; context thin, submembranous, discolored, odorless, mild; lamellae squarely adnate, rather broad, inserted, medium distant, entire, avellaneous; cystidia none; spores ellipsoid, smooth, hyaline, about 6×4 μ; stipe enlarged at the apex, smooth or striate, pruinose, avellaneous, $3–4 \times 0.2–0.3$ cm.

Type collected by Erdman West on his lawn in Gainesville, Fla., June 3, 1938 (*F 18279*). Also collected by W. A. Murrill on open grassy lawns or shaded soil in Gainesville from July to October, 1938 (*F 18283, F 18288, F 18284*). A typical member of this large and difficult genus, occurring at times in abundance.

Marasmiellus oligocinsulae sp. nov. Pileo dimidiato, conchato, 1–2 cm. lato, glabro, isabellino; lamellis distantibus, adnatis, subconcoloribus; sporis ellipsoideis, $8–10 \times 4–5$ μ.

Pileus membranous, short-stipitate or vertically attached, subcircular or dimidiate, conchate, gregarious, 1–2 cm. broad; surface glabrous, rugulose, striate at times, uniformly isabelline or rosy-isabelline to fulvous, margin entire; context thin, tough, reviving, concolorous, slightly astringent; lamellae few, adnate, broad, distant, inserted, some forked at the base, entire, pale rosy-isabelline; spores ellipsoid, smooth, hyaline, granular, $8–10 \times 4–5$ μ; cystidia none; stipe short, curved, eccentric, smooth, glabrous, concolorous to dark-brown or blackish.

Type collected by West and Murrill on a dead grapevine in Planera Hammock, eleven miles northwest of Gainesville, Fla., July 20, 1938 (*F 17944*). Also collected on the same host by W. A. Murrill in woods at Gainesville, Sept. 1, 1938 (*F 18296*). Suggesting *Scytinotus concolor* (Berk. & Curt.) Murrill, but not resupinate when young, usually provided with a stipe, and not coriaceous.

NEW COMBINATIONS

For those using Saccardo's nomenclature the following new combinations are made.

Gymnopus aurantiacus = **Collybia aurantiaca**
Gymnopus castaneidiscus = **Collybia castaneidisca**
Gymnopus floridanus = **Collybia floridana**
Gymnopus mammillatus = **Collybia mammillata**
Hydrocybe subruber = **Hygrophorus subruber**
Marasmiellus oligocinsulae = **Marasmius oligoinsulae**

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A Definition of the Genus Brodiaea

ROBERT F. HOOVER

The genus *Brodiaea* is a group of widely varying content as treated by various authors. When first published in 1811, two species were indicated, *B. grandiflora* and *B. congesta*, both of which had been published previously, as *Hookera coronaria* and *Hookera pulchella* respectively. Numerous species of quite diverse nature were added at intervals until J. G. Baker, in an article published in 1896, included forty-five species native to both North and South America. It is to be noted, however, that Baker's classification of 1896 was not the result of original research in the group at that time, but according to the author's statement was an enumeration of the species which would be included in *Brodiaea* as that genus was defined in Bentham and Hooker's "Genera Plantarum." In contrast to this treatment is that of Abrams, who in his "Illustrated Flora of the Pacific States" recognizes six genera in these three states alone for the plants included in *Brodiaea* by Baker, and leaves only eight species in *Hookera* (which includes the type species of *Brodiaea*). Such wide divergence of opinion indicates clearly to the writer that a final solution of the problem can not come from discussion of the characters by means of which early authors distinguished their genera, but only from a study of the plants themselves with the purpose of evaluating all their differences, whether previously mentioned in the literature or not.

The first question to be answered in arriving at a satisfactory classification of this group is whether species from North and South America can be referred to the same genus. The jointed pedicels of the North American as contrasted with the unjointed pedicels of the South American species constitute a difference which is readily observed. Evidently the first author to emphasize this difference was Watson. Greene also mentioned this character, but most other writers have not considered it of value in distinguishing genera in this group, and some have neglected even to mention it. To one who is influenced by considerations of plant geography, such a well-defined and constant difference is of great importance. However, the two groups of species need not be distinguished by that character alone.

Without exception, all of the North American species which have been customarily referred to *Brodiaea* have solid somewhat globose fibrous-coated corms. In contrast, every South American species which the writer has examined has elongated tunicated membranous-coated bulbs, although

specimens of many were not available,[1] and the leaves, unlike those of any North American species, have broad membranous sheathing bases continuous with the coats of the bulbs. The South American species also have an involucre which is termed "spathaceous"; that is, it consists of one or two ascending bracts, as in many species of *Allium*. In the North American plants the bracts are spreading and their number is always more than two, appearing to be correlated to some extent with the number of flowers in the umbel. Since no exceptions to these fundamental contrasts have been noted, the writer believes that the generic distinctness of the South American plants from the North American *Brodiaea* can be no longer in doubt. None of the distinguishing features if taken alone is necessarily decisive, but their constant association is too impressive to be ignored.

Although it is here necessary, because of lack of fresh material, to restrict the differentiation between North American and South American plants to the characters stated above, there are doubtless other differences. The writer has been able to study fresh plants of one South American species, the so-called "*Brodiaea uniflora*." In addition to the features noted as distinctive of all South American species, it has broad flat leaves of a sort never seen in a North American *Brodiaea*. The peculiar succulence of the herbage is also unknown in the North American forms. Most notable of all, "*Brodiaea uniflora*" has a strong alliaceous odor. The importance of such a character has been discussed in an article by Greene (Pittonia **2**: 51–57). If such plants are merged with *Brodiaea*, there can hardly be any logical reason for excluding *Allium* or *Agapanthus*, or indeed for not regarding the Allioideae as a single genus.

Although the above evidence indicates that the South American species under consideration should not be included in *Brodiaea*, their true generic status remains in doubt. Most of them were referred by early authors to *Milla*, a genus which Baker in 1896 restricted to the original Mexican species. Watson (Proc. Am. Acad. **14**: 285) and also Greene suggested that the South American plants are properly referred to *Leucocoryne*, although they have six stamens as contrasted with the three stamens alternating with staminodia of typical members of *Leucocoryne*. Perhaps *Milla* and *Leucocoryne* should not be distinguished from each other as genera. Engler recognized both genera but also mentioned South American species under *Brodiaea*. However, the one species listed by him, *B. uniflora*, does not answer to his key character "Blh. trichterförmig oder glockig" but is

[1] The following South American species, named under *Brodiaea*, were examined: *B. Felipponei*, *B. porrifolia*, *B. Speggazinii*, *B. Tweediana*, *B. uniflora*.

rather "präsentiertellerförmig," hence referable to *Milla* in Engler's classification. This problem of generic identity is one which should be undertaken by field students in the countries where the plants are native. It can never be accurately solved by study of herbarium specimens alone.

J. F. Macbride, in an article published in 1918, in addition to retaining in *Brodiaea*, at least by implication, all plants previously referred there, included also *Androstephium*, a procedure which evidently has not met with acceptance by subsequent authors. Macbride's discussion was limited to remarks indicating that the flower characters on which earlier botanists had based genera were of no importance. No mention was made of the nature of the corms or bulbs, or of possession or lack of alliaceous properties. It is true that the flowers of all Allioideae are similar in general structure, but most botanists have admitted the importance of differences in other parts of the plant and in the individual parts of the flower.

As accepted by most modern botanists, the name *Brodiaea* has come to be applied to a large group of species native to western North America, characterized as a whole by a tubular perianth with one-nerved segments, jointed pedicels, distinct filaments, and lack of alliaceous properties, as distinguished from the genera of the subfamily Allioideae to which it seems most nearly related. This concept of the genus appears to have been first approached by Sereno Watson, but *Stropholirion* and *Brevoortia*, which Watson recognized as genera, are now usually included in *Brodiaea*. Popular usage generally has adopted this definition of *Brodiaea*.

From an early date various genera were segregated from this group under such names as *Dichelostemma*, *Triteleia*, *Hesperoscordum*, *Calliprora*, and *Seubertia*, but it remained for E. L. Greene, in an article published in 1886, to arrange these various segregates into a natural classification. It was evident to Greene, as a field student in western North America, that *Brodiaea* in the generally accepted sense consisted of three distinguishable groups of species. To these he applied the generic names *Triteleia*, *Hookera*, and *Brodiaea*. In *Triteleia*, typified by *T. grandiflora* Lindl., were included the segregate genera *Seubertia*, *Calliprora*, and *Hesperoscordum*. *Brodiaea congesta* Smith was regarded as the type species of *Brodiaea*, and in that genus were included *Dichelostemma* and *Macroscapa*, the latter being known also as *Stropholirion* and *Rupalleya*. The remaining species, those related to *Hookera coronaria*, were left under the name *Hookera*. In his "Flora of California," W. L. Jepson distinguished these same three groups but regarded them as subgenera under *Brodiaea* rather than as genera. In addition, the segregate genus *Brevoortia* was included in the subgenus *Dichelostemma*.

From field studies it was early evident to the writer that all three groups recognized by Greene and by Jepson were fundamentally natural, and that an attempt to divide any of them further resulted in separation of clearly related entities. It was also seen, even though the plants of each group had undefined features of aspect which rendered these groups readily distinguishable in the field, that the differences mentioned by Greene and other botanists could hardly be regarded as of generic value. Accordingly, a search was made for characters which might satisfactorily determine whether *Brodiaea* of common usage is actually one genus or three. Several such characters were immediately found, of which there appeared to be no published record.

Without exception, the species of *Triteleia*, as that genus was defined by Greene, have corms with pale fibrous coats, while the corm-coats of the other species are dark brown. This constant and easily observed difference in color probably indicates some difference in chemical composition, one of the most reliable indications of true relationship. The leaves of the *Hookera* group are always rounded on the back and show no external trace of a midrib, while both *Triteleia* and *Dichelostemma* have leaves which are keeled on the back and with two parallel longitudinal impressions on the upper surface. This leaf difference is quite obvious in living plants and probably has been neglected because the leaves often wither before the flowering season. Compound umbels occasionally found on teratological plants suggest that the inflorescences of these groups of species are perhaps not exactly homologous. In every species of *Triteleia*, in contrast with *Hookera* and *Dichelostemma*, the anthers are versatile and never appressed to the style. The position of the stamens with respect to the style is obscured in pressing but in fresh flowers is obvious. A notable difference between the three groups was found in the structure of the stigma. Finally, in 1937, the seeds of several species were collected. A study of these confirmed Greene's conclusions of 1886 in a truly surprising manner and, in combination with other features, fully convinced the writer of the validity of the three genera recognized by Greene.

As *Brodiaea* is now a conserved name under the International Rules, with *B. grandiflora* Smith (*Hookera coronaria*) as its type species, the name *Brodiaea* must now be applied to the genus called by Greene *Hookera*. Accordingly, *Brodiaea* as understood by Greene becomes *Dichelostemma*, while *Triteleia* is accepted exactly as defined by Greene in 1886. The distinctive characters of the three genera are summarized as follows:

Corm-coats straw-color; leaves flattened, carinate; inflorescence when compound with pedicels arising from a structure which in position and

appearance simulates the perianth of one of the flowers of the primary umbel; anthers versatile, not sagittate, not appressed to style; stigma not evidently lobed; seeds as thick as long or nearly so, rounded, coarsely pitted and minutely granulate, with prominent longitudinal ridge on one side . . . . *Triteleia.*

Corm-coats dark brown; leaves flattened, carinate; compound inflorescences essentially as in *Triteleia;*[2] anthers basifixed, slightly notched at base, erect and closely appressed to style; stigma slightly three-lobed, the lobes not spreading, continued downward as wings on upper portion of style; seeds much longer than thick, longitudinally striate, sharply three-angled, with ridges of equal prominence on all the angles . . . . *Dichelostemma.*

Corm-coats dark brown; leaves rounded, not carinate; inflorescence when compound with scape branching and bearing two normal umbels and often additional solitary flowers, never with a peduncle arising from a perianth-like structure; filaments attached on back of anthers immediately above the distinctly sagittate base; anthers erect and closely appressed to style; stigma three-lobed, the lobes spreading and recurving; seeds slightly longer than thick, obtusely angled, longitudinally striate, with ridge on one side moderately developed. . . . . *Brodiaea.*

Since specimens of every known species of these three genera have been examined by the writer, it may be stated confidently that, except possibly in seed characters, there are no exceptions, in the species so far discovered, to the generic characters listed above. The seeds of all species of *Brodiaea* and *Dichelostemma* are as here described, but the seeds of a few species of *Triteleia* were not available. In addition may be noted the well-known facts that *Triteleia* has six stamens alike except sometimes in size, *Dichelostemma* has the alternate stamens either greatly modified or transformed into staminodia, and *Brodiaea* has always three stamens alternating with staminodia. It is of interest that on the basis of all the above characters, including seed characters, *Calliprora* and *Hesperoscordum* are both quite typical of *Triteleia*, while *Stropholirion* and *Brevoortia* are typical members of *Dichelostemma.* When various distinctive features are correlated in this manner without any known exceptions, the evidence in regard to generic limits seems conclusive. Accordingly, it is suggested that in scientific usage the name *Brodiaea* be limited to the group of species here characterized as that genus, although the well-established use of "Brodiaea" as a common name for other species, if not misunderstood, can conveniently be continued.

Cytologic studies possibly would indicate some correlation between the chromosomes of the three genera and their morphologic characters,

[2] The writer has observed no compound umbels in *Dichelostemma*, but their occurrence in *D. capitatum* has been described by Greene (Bull. Cal. Acad. **2**: 135).

but the available results are not conclusive. Four species of *Dichelostemma* and four of *Brodiaea* were investigated by D. A. Johansen. The results, published in 1932, show the diploid chromosome number in the various species of *Dichelostemma* to be 30, 36, 36, and 72, as compared with 10, 12, 14, and 42 in *Brodiaea*. *Brodiaea* thus has generally fewer chromosomes, but that difference is not consistent. No statements have been published regarding the comparative morphology of the chromosomes.

Finally, something should be said regarding the general principle involved in distinguishing *Dichelostemma* and *Triteleia* from *Brodiaea*. There is always a tendency to disregard genera which are thought to depend on intangible features rather than on formal "characters." The results here outlined, the writer believes, indicate that if a search is made some constant and readily observable character can often be found. Similar studies probably would produce comparable results in many groups of plants where readily recognizable genera seem deficient in morphological characters.

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A Note on the Morphology of the Deciduous Shoot of Taxodium distichum

G. L. Cross

(with 6 figures)

With the exception of the papers of Coulter (1889) detailed morphological studies of the shoot of *Taxodium* Rich. apparently are lacking. An early treatment of the gross structure of the twigs was published by Henry (1837), who described the varying phyllotaxy (2/5 to 5/13) and noted the occurrence of axillary and adventitious buds. Henry was especially interested in the foliar organs of the adventitious shoots, and mentioned the important fact that certain shoots are deciduous at the end of the growing season while others are permanent. His observations were confined to a single tree which grew in the botanical garden at Bonn.

A somewhat more recent treatment of *Taxodium* is that of Velenovský (1905), who described the sympodial nature of the shoots, and pointed out the resemblance of the deciduous shoot to the compound leaf of a fern. Velenovský stressed the fact that in these respects *Taxodium* resembles *Glyptostrobus* and certain fossil species of *Sequoia*.

The deciduous shoots are a noteworthy feature of *Taxodium*. They are commonly three or four inches long, but under certain conditions may elongate to seven or eight inches. There are differences of opinion concerning their interpretation. Prominent among these are the contrasting opinions of Bernard (1926) and Doak (1935). Bernard regards the deciduous shoots as homologous with the dwarf shoots of *Pinus*. However, Doak reports: "The situation in *Taxodium* . . . is more complex. Here the portion of the dwarf shoot which is homologous to the dwarf shoot of pines is partly imbedded and may be exposed by stripping away the bark. These dwarf shoots branch repeatedly from lateral buds which occur at the base of the current growth. The resulting deciduous shoots are homologous to a proliferated dwarf shoot of pine and not to the ordinary dwarf shoots as interpreted by Bernard."

A recent study of an abundance of preserved and living material[1] has convinced this writer that the interpretation of Bernard is somewhat more satisfactory than that of Doak.

[1] Materials were collected principally from trees growing on the campus of the University of Oklahoma, but several collecting trips, financed by a University Research Grant, were made into southeastern Oklahoma (McCurtain County) where *T. distichum* Rich. occurs extensively. A form with acicular leaves, probably *T. ascendens* Brong., also was collected in southeastern Oklahoma. It is hoped that comparative studies of the two species may be made.

The Permanent Shoots.—The permanent shoots originate as lateral (rarely terminal) globose buds in the axils of the uppermost scale-leaves of the current year's growth. Two to several buds are produced near the tip of each twig, one of which will ultimately develop while the rest usually die back. Terminal buds are infrequently formed on the permanent shoots, but these either abort or develop into shoots which die and dry back to their juncture with the first axillary branch. The resulting sympodial type of branching is unique among conifers (Velenovský, 1905).

In winter the bud of each permanent shoot consists of a short axis upon which are numerous imbricate, ovate, acute, carinate scales. Enclosed within the scales is a series of scale-leaves. In the axils of some of the younger scale-leaves are often found primordia of deciduous shoots which will develop and expand with the parent bud.

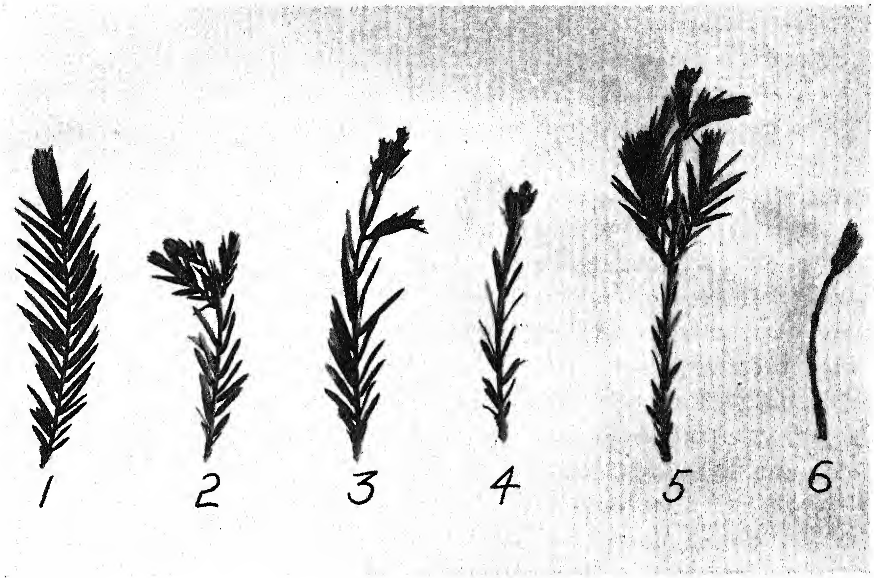
When the winter buds of the permanent twigs expand, the internodes elongate rapidly and the scale-leaves increase in size. The primordia of the axillary deciduous shoots likewise begin growth, and buds of the permanent shoots for the succeeding year are initiated in the axils of the uppermost scale-leaves. The scales and scale-leaves of the permanent twig are persistent during the summer. In the autumn the scale-leaves and most of the scales usually fall, but at the base of the twig a few of the scales persist during the winter and may be retained during a portion of the second growing season. In the axils of those upper scale-leaves which lack currently expanding deciduous shoots, or secondary permanent shoots, resting buds of deciduous shoots are formed pseudo-endogenously.[2] These grow and soon rupture the cortex and epidermis just above the juncture of the scale-leaf and the stem. Endogenous adventitious winter buds of deciduous shoots, apparently arising in cortical tissues, are formed near the bases of many of the scale-leaves.

The Deciduous Shoots.—The deciduous shoots may be divided, on a basis of time and place of origin, into several groups, viz., (1) those which arise exogenously in the axils of the upper scale-leaves of the expanding permanent twig, and expand with the parent twig; (2) those which are formed pseudo-endogenously in the lower scale-leaves of the permanent twig; (3) those which arise endogenously near the bases of the lower scale-leaves and scales of the permanent twig; and (4) those which arise endog-

[2] These buds appear to arise endogenously, but investigation has revealed that their primordia are formed from surface tissue which is left at the bottom of depressions or crevices formed by the upgrowth of the surrounding tissues in the axils of the scale-leaves. The primordia are formed in the summer. The mechanics and time of their formation is now being investigated by the writer.

enously?) in the axils of the lower scales of pre-existing deciduous shoots. For convenience in discussion, these four categories may be consolidated into two main groups, i.e., exogenous types and "endogenous" (including pseudoendogenous) types.

The exogenous and "endogenous" buds of deciduous shoots differ markedly in structure. In the winter condition the "endogenous" buds occur as small globose structures consisting of an axis upon which are numerous, linear-lanceolate, apiculate, foliage leaves enclosed by two or



Figs. 1 and 2. Deciduous shoots. $\times\frac{2}{3}$. Fig. 3. Probably a deciduous shoot. $\times\frac{2}{3}$. Figs. 4–6. Permanent shoots. $\times\frac{2}{3}$.

more opposite or nearly opposite, broadly-ovate bud scales. The leaves immediately above the two bud scales are reduced in size and apparently transitional between the bud scales and foliage leaves. The exogenous buds, occurring as components of larger compound buds, do not have the two basal scales.

At the time of bud expansion the internodes of the deciduous shoots elongate and the leaves enlarge until a twig several centimeters long is produced. Usually no branches or buds are formed in the axils of the leaves of the deciduous shoots (except in the axils of the basal scales), but occasionally the deciduous shoots proliferate exogenously from the axils of their median or upper leaves (fig. 2). Such proliferation occurs most

frequently from deciduous shoots that are distally located near expanding permanent twigs. The proliferating deciduous shoots are quite variable in form and structure. Some resemble permanent shoots and a transitional series can be found readily on any tree (fig. 1–6). Figure 1 is a photograph of an axillary deciduous shoot which had formed near the base of a one-year-old permanent twig. It shows no indication of proliferation. Figure 2 is an axillary deciduous shoot which was more distally located on a permanent twig. It shows extensive proliferation from its terminal portions. Figure 3 is an axillary shoot, (probably deciduous) of a type frequently found expanding near the tip of one year old twigs. It has proliferated extensively, and three buds have formed at its tip. Twigs of this type when observed throughout a growing season were some times found to be deciduous and some times permanent. Figures 4–6 are photographs of various types of permanent shoots. Figures 4 and 5 show twigs with well formed leaves. Figure 6 illustrates a twig with scale-leaves of the type commonly described for *Taxodium*. This series of figures indicates that the deciduous and permanent shoots of *Taxodium* are equivalent. Physiological variations which probably may be correlated with varying positions on the branch apparently cause some twigs to absciss and others to become permanent.

All deciduous shoots fall from the tree annually. This is accomplished by the formation of abscission layers comparable in origin and structure to the abscission layers developed by the deciduous leaves of angiosperms (Bernard, 1926). In the case of the deciduous shoots of exogenous origin the abscission layer forms below the lowest foliar appendage, and the entire shoot falls cleanly, leaving no basal portion. However, the deciduous shoots of "endogenous" origin develop their abscission layers above the lowest scales, and the latter with a portion of the axis, is left as an integral part of the main branching system. In the axil of one of the basal scales is formed an "endogenous" bud of a deciduous secondary shoot which will expand the next season.

The difficulty of interpreting deciduous shoots of such diverse origin, structure, and developmental behavior, in terms of the dwarf shoots of *Pinus*, is apparent.

The dwarf shoots of *Pinus* are of exogenous origin. They arise as parts of a compound bud in the axils of scale-leaves which are born on the axis of a permanent twig. Their growth in length is ordinarily determinate, but occasionally they may proliferate. Proliferation is achieved as a result of renewed meristematic activity in the apex of the dwarf shoot. The pro-

liferated axis is, therefore, a continuation of the axis of the dwarf shoot.

Homology implies a likeness in origin, position, structure, and value. When we examine *Taxodium* for structures which are alike in origin, position, etc., to the dwarf shoots of *Pinus*, it becomes apparent that the exogenous deciduous shoots which are formed as components of the expanding bud of *Taxodium* are structures which show this correspondence. The only significant differences between these two types of shoots are that the deciduous shoots of *Taxodium* are annual while those of *Pinus* are perennial, and the dwarf shoots of *Taxodium* proliferate laterally while those of *Pinus* proliferate apically. Thus the exogenous deciduous shoots of *Taxodium* might be regarded logically as homologous to the dwarf shoots of *Pinus*. Since the other deciduous shoots of *Taxodium* differ from the exogenous ones mainly with respect to time of formation, being similar in other respects, the writer can see little objection to regarding all deciduous shoots of *Taxodium* as equivalent or homologous to the dwarf shoots of *Pinus*.

Doak's (1935) statement that the dwarf shoot of *Pinus* is homologous to a dwarf shoot of *Taxodium* which is imbedded in the bark of the parent twig, seems untenable. The imbedded shoot of *Taxodium* arises somewhat as follows: An axillary or an adventitious deciduous shoot is formed which has a pair (or more) of fleshy scales at its base. During the expansion of this first deciduous shoot, a bud of a secondary deciduous shoot is formed in the axil of one of the scales of the first shoot. At the end of the growing season the first deciduous shoot abscisses in a plane above the fleshy scale with its axillary bud. The next spring the second deciduous shoot expands and in the axil of one of its scales the bud of a third deciduous shoot is formed, and so on for a variable number of years. It will be seen that each successive deciduous shoot leaves its basal portion as an integral part of a sympodially branched dwarf shoot system. This dwarf shoot system does not form a terminal bud, for the terminal portion abscisses each year. The behavior in this respect closely parallels that exhibited by the long branches, where the terminal shoots, when formed, die back. Clearly a dwarf branch system consisting of the basal portions of several, successive, axillary deciduous shoots and devoid of an apical meristem, cannot be considered homologous with the simple unproliferated dwarf shoot of *Pinus*.

The factors responsible for the interesting variations in the time, place and method of formation of the deciduous shoots of *Taxodium* present a puzzling problem. It is hoped that detailed histogenetic studies, together

with experimental work now in progress at the University of Oklahoma, will provide information which may contribute to a clarification of the problem.

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Studies in the Uredinales, the Genus Maravalia[1]

E. B. Mains

The genus *Maravalia* was proposed by Arthur (1922) based on *Maravalia pallida* Arth. & Thaxter. This species was described from a collection made by R. Thaxter on *Pithecolobium latifolium* in Trinidad. The telia are subepidermal and the teliospores are one-celled, with very thin, hyaline, smooth walls, pedicellate, arising from a compact hymenium. Arthur (1922) pointed out that *Chaconia*, which was described by Juel from *Pithecolobium*, differed in that the latter has sessile teliospores clustered on basal cells. He concluded that *Maravalia* was apparently a short-cycled *Spirechina.*

Jackson (1931) has shown that *Spirechina Loesneriana* (P. Henn.) Arth., the type species of *Spirechina*, has teliospores in chains and is a species of *Kuehneola*. For the other species on Rubus which have one-celled, colorless, pedicellate teliospores and which had been included in *Spirechina* he proposed the name *Mainsia.* Jackson also has pointed out that in species of *Mainsia* the pycnia, uredinia, and telia are intraepidermal. *Mainsia* apparently includes a group of closely related species limited to *Rubus*. *Maravalia* is, therefore, apparently not a short-cycled *Mainsia.*

Since the establishment of the genus Maravalia, 7 species have been added, namely: *M. hyalospora* (Sawada) Dietel, *M. albescens* Syd., *M. utriculata* Syd., *M. achroa* (Syd.) Arth. & Cummins, *M. Crotolariae* Syd., *M. Hygrophilae* (Syd. & Butler) Mains, and *M. ascotela* (Syd.) Mains. It has been shown elsewhere (Mains, 1939) that *M. utriculata* has sessile teliospores and is *Bitzea Ingae* (Syd.) Mains.

In *Maravalia pallida* the walls of the teliospores are very thin. There is no definite germpore. When germination starts there is an apical prolongation. The basidium appears to be a prolongation of the teliospore. As Arthur has pointed out, the teliospores arise from a compact hymenium and are not grouped on laterally free basal cells. A similar condition occurs in *M. achroa*, *M. Hygrophilae*, and *M. ascotela*. In *M. hyalospora* and *M. Crotolariae,* although a germpore is not apparent in the teliospore previous to germination, when germination takes place a pore can be dis-

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tinguished and there is a definite differentiation between the wall of the basidium and the wall of the teliospore.

Maravalia has been placed in the tribe Ravenelieae by Dietel (1928). Apparently this disposition was based on his interpretation (1924) of the teliospores of *M. albescens*. In this species he considered that often two teliospores developed from a pedicel. As has been shown elsewhere (Mains 1938 b) the one-celled teliospores of the type of this species develop in groups from laterally free basal cells. The teliospores develop in succession from these cells. The basal cells are not pedicels but sporogenous cells and *M. albescens* is *Chaconia alutacea*. The teliospores of *Maravalia* arise singly from a compact hymenium and *Maravalia* therefore does not belong in the Ravenelieae.

Dietel (1928) has recognized a tribe, Eriosporangieae, in which he includes genera which have one- or two-celled pedicellate teliospores which arise singly, germinate immediately and have colorless or pale brown walls. In this he places the genus *Argomycetella* Syd. in which he includes species having one-celled teliospores with very thin colorless smooth walls, germinating immediately. *Poliotelium* Syd. is considered synonymous.

Sydow (1922) proposed *Argomycetella* for species having uredinia and telia and *Poliotelium* for species having aecia and telia. *Argomycetella pressa* (Arth. & Holw.) Syd. was selected as the type species and *A. dolichospora* (Diet. & Holw.) Syd. was included. *Argomycetella pura* Syd. has been described since. Apparently only one species has been placed in *Poliotelium*, *P. Iresines* (Lagerh.) Syd. *Argomycetella pressa* and *A. pura* have very thin-walled teliospores without evident germpores, apparently germinating by a prolongation of the apex of the spore. In *A. dolichospora* and *Poliotelium Iresines*, a definite pore is evident when the teliospores germinate.

There seems to be no generic distinction between *Maravalia* and *Argomycetella*. *Maravalia* was published by Arthur (1922) in the Botanical Gazette in January 1922 and *Argomycetella* by Sydow (1922) in September 1922, the latter therefore, becomes a synonym. From *Poliotelium* on the other hand, *Maravalia* can be separated by the manner of the germination of the teliospores, *Maravalia* including those species in which the teliospores germinate without an evident pore by the prolongation of the apex, and *Poliotelium*, those species in which germination takes place through a pore. This distinction necessitates a realignment of the species which have been assigned to *Maravalia* and *Argomycetella*.

In this interpretation *Poliotelium* is not based on life-cycle. It parallels *Eriosporangium*, having one-celled instead of two-celled teliospores. There

has been considerable difference of opinion whether *Eriosporangium* should be separated from *Puccinia* and the same question arises concerning *Poliotelium* in relation to *Uromyces*. Dietel (1928) recognizes *Eriosporangium* for species having aecia without or with poorly developed peridia and teliospores with pale or colorless walls, germinating at once. As has been pointed out by Jackson (1932) there are species which are intermediate between *Eriosporangium* and *Puccinia*. This, however, is to be expected for two closely related genera having many species. It is believed that they should receive generic status. Consequently the following species should be included in the genus *Poliotelium*: *Poliotelium Iresines* (Lagerh.) Syd. (type), **Poliotelium hyalospora** (Sawada) comb. nov., **Poliotelium dolichosporum** (Dietel & Holw.) comb. nov. The type of germination of the teliospore would also place *Maravalia Crotolariae* here. However, in this species the teliospores develop in groups from laterally free basal cells. It does not fit well into any of these generic groups.

In the course of these studies, another species, *Uromyces elatus* Syd. has been found to have teliospores which evidently place it in *Maravalia*. This species is of special interest since it possesses aecia. Of the species proposed for the genus *Maravalia*, *M. pallida* and *M. Hygrophilae* have had only telia described; *M. achroa* uredinia and telia; *Argomycetella pressa* and *A. pura*, pycnia, uredinia and telia; *M. ascotela* pycnia and telia. *Uromyces elatus* has pycnia, aecia, and telia. The aecia have well developed peridia. This is not in agreement with the majority of the rusts having colorless teliospores. Whether this will hold for all future species remains to be seen. The following revision of the genus *Maravalia* is proposed.

MARAVALIA, Arth. Bot. Gaz. **73**: 60. 1922.

Argomycetella Syd. Ann. Mycol. **20**: 124. 1922.

Pycnia subepidermal. Aecia subepidermal, flat, with peridia; aeciospores verrucose, catenulate. Uredinia subepidermal; urediniospores echinulate, pedicellate. Telia subepidermal teliospores one-celled, pedicellate, germinating immediately, the wall hyaline, very thin, germinating by apical prolongation of the wall without evident pore, laterally free, arising singly from a compact hymenium.

Types species: *Maravalia pallida* Arth. & Thaxter.

MARAVALIA PALLIDA Arth. & Thaxter, Bot. Gaz. **73**: 60. 1922.

Telia hypophyllous, crowded in large groups, subepidermal, ruptured epidermis evident, soon white from germination; teliospores clavate or clavate-oblong, $16–22 \times 52–70\mu$, the walls hyaline, very thin, 0.5μ or less, the pedicels $8–10 \times 20–35\mu$.

Specimen examined: *Pithecolobium latifolium* (L.) Benth. Maraval Valley, Trinidad, April 1913, R. Thaxter (type). Reliq. Farl. 676.

This species is known only from the type collection.

MARAVALIA ACHROA (Syd.) Arth. & Cummins, Phil. Journ. Sci. **61**: 468. 1936.
Uromyces achrous Syd. Ann. Mycol. **5**: 491. 1907.

Uredinia mostly hypophyllous, scattered, yellowish, pulverulent; urediniospores obovoid or ellipsoid, 14–16×16–20μ, the walls colorless, 1μ, moderately echinulate, the pores obscure.

Telia mostly hypophyllous or caulicolous, scattered, pulvinate, waxy; teliospores oblong or obovoid, 9–13×22–32μ, the walls hyaline, thin 0.5μ, the pedicels colorless, 3×18–28μ.

Specimens examined: *Dalbergia Sissoo*, Pusa, Dec. 19, 1906, E. J. Butler (877, type); *Dalbergia* sp. Bosoboso, Rizal, Luzon, P. I. Feb. 11, 1924, Clemens (1701).

This species is apparently known only from India and the Philippines.

Maravalia elata (Syd.) comb. nov.

Uromyces elatus Syd. Ann. Mycol. **6**: 482. 1908.

Pycnia mostly epiphyllous, in small groups deeply seated in the host tissue, globoid, 160–200μ in diameter, ostiolar filaments projecting.

Aecia mostly hypophyllous, in groups associated with the pycnia or scattered singly or in small groups without pycnia, the hymenium flat, circular in outline, large, 0.8–1.0 mm. across, bordered by well developed peridia; peridial cells thin, difficult to study, in face view 22–43×26–56μ, somewhat loosely attached; aeciospores subgloboid, 19–26×26–35μ, the wall colorless, 2–2.5μ, closely and finely verrucose.

Telia hypophyllous, small, 0.2 mm. across, crowded in groups up to 5 mm. across, white; teliospores cylindric or cylindric-ovoid, 13–20×40–68μ, the wall hyaline, very thin, 0.5μ, the pedicel hyaline, up to 50μ long.

Specimens examined:

Lupinus paniculatus Desv. Cuzco, Peru, June 29, 1920, E. W. D. and Mary M. Holway (738); La Paz, Bolivia, March 18, 1920 and May 14, 1920, E.W.D. and Mary M. Holway (417, Rel. Holw. 247; 603, Rel. Holw. 259).

Lupinus saxatilis Ulbrich, La Paz, Bolivia, Aug. 12, 1914, Mr. and Mrs. J. N. Rose (18863).

Lupinus soratensis Rusby, Sorata, Bolivia, April 22, 1920, E.D.W. and Mary M. Holway (561, Rel. Holw. 255).

Lupinus tomentosus D.C. Pampa de Arrieras, Peru, Aug. 23, 1914, Mr. and Mrs. J. N. Rose (18962).

Lupinus sp. La Paz, Bolivia, March 24, March 25 and May 12, 1920, E.W.D. and Mary M. Holway (454, Rel. Holw. 248; 459, Rel. Holw. 249; 595, Rel. Holw. 257).

The species was originally described from a specimen collected by O. Buchtien on *Lupinus ramossimus* at La Paz, Bolivia on Aug. 19, 1906. It is apparently known only from Bolivia and Peru. Although the aecia have peridia they are very large and have a flat hymenium, in these respects resembling aecia of the rusts with colorless teliospores. Apparently both primary and secondary aecia are produced.

MARAVALIA HYGROPHILAE (Syd. & Butler) Mains, Am. Journ. Bot. **25**: 678. 1938.

Blastospora Hygrophilae Syd. & Butler, Ann. Mycol. **10**: 265. 1912.

Telia amphigenous, mostly hypophyllous, crowded in small groups 2–4 mm. across, pulvinate, cinereous from germination; teliospores broadly ellipsoid, 12–16×28–32μ, the wall smooth, hyaline, 0.5μ, the pedicel fragile, broad, up to 8μ.

Specimen examined: *Hygrophila salicifolia*, Chittagong, India, Sept. 9, 1911, R. Sen, type.

As discussed elsewhere (Mains, 1938a) the telia of Blastospora are superstomatal. Apparently this species is known only from the type collection.

MARAVALIA ASCOTELA (Syd.) Mains, Am. Journ. Bot. **25**: 678. 1938.

Blatospora ascotela Syd. Ann. Mycol. **33**: 52. 1935.

Pycnia amphigenous, subepidermal, deep seated in the host tissue, spherical, 100–160μ in diameter.

Telia hypophyllous, 0.1–0.2 mm. across, densely grouped about the pycnia, subepidermal, pulvinate, waxy; teliospores cylindric, 13–16×56–70μ, the wall very thin, 0.5μ, hyaline, smooth, the pedicels hyaline, thin-walled, 6×20–30μ.

Specimen examined: *Hedyotis stylosa* Brown, Ootacamund, British East India, Dec. 6, 1932, J. R. Mitten (107, type).

Maravalia pressa (Arth. & Holw.) comb. nov.

Uromyces pressus Arth. & Holw. Mycologia **10**: 125. 1918.

Argomycetella pressa Syd. Ann. Mycol. 20: 124. 1922.

Pycnia not seen. Arthur and Holway (l.c.) state that they were found sparingly on one specimen, describing them as epiphyllous, subepidermal, globoid, 110μ in diameter.

Uredinia mostly hypophyllous, scattered or in small groups, subepidermal; urediniospores ellipsoid, 21–26×27–32μ, the wall yellowish or pale cinnamon, 2.5–4μ thick, moderately echinulate, the pores 3, equatorial.

Telia hypophyllous, scattered or in small groups, subepidermal, white; teliospores oblong or oblong-ellipsoid, 16–18×29–35μ, the wall hyaline, thin, 0.5μ, the pedicel hyaline, up to 20μ long.

Specimens examined:

Vernonia Deppeana Less. San Lucas, Toliman, Solola, Guatemala, Feb. 2, 1915, E.W.D. Holway (173); Malacatancito, Huehuetenango, Guatemala, Jan. 24, 1917, E.W.D. Holway (779); Cartago, Costa Rica, July 2, 1923, F. L. Stevens (202); San Jose, Costa Rica, Jan. 3, 1916, E.W.D. Holway (361, type); El Alto, Costa Rica, Jan. 16, 1916, E.W.D. Holway (432); Cartago, Costa Rica, Jan. 20, 1916, E.W.D. Holway (450).

Vernonia sp. San Ramon, Costa Rica, Jan. 13, 1916, E.W.D. Holway (413).

Maravalia pura (Syd.) comb. nov.

Argomycetella pura Syd. Ann. Mycol. **23:** 313–314. 1925.

Pycnia amphigenous, mostly epiphyllous, in small groups, subgloboid, 80–100×100–120μ, deep seated in the host tissue.

Uredinia mostly hypophyllous, grouped about the pycnia or scattered, subepidermal, pale cinnamon; urediniospores obovoid or ellipsoid, 18–23×26–32μ, the wall 1.5–2μ, cinnamon, moderately echinulate, the pores 2, equatorial.

Telia hypophyllous, subepidermal, scattered, white; teliospores oblong or ovoid, 16–18×28–34μ, the wall hyaline, thin, 0.5μ or less, the pedicel hyaline, up to 30μ long.

Specimen examined: *Vernonia patens* H.B.K. La Caja, San Jose, Costa Rica, Jan. 6, 1925, H. Sydow (type).

This species is closely related to the preceeding, differing in having urediniospores with thinner walls and fewer pores.

In Dietel's classification (1928) *Marvalia* should be placed in the tribe Eriosporangieae, on account of the pedicellate teliospores. However, *Chrysocyclus*, placed by Dietel in the Eriosporangieae, and *Maravalia* are very similar to genera of the Oliveae in teliosporic characters, a tribe which Dietel has placed some distance from the Eriosporangieae. With *Chrysocelis* of the Oliveae they apparently form a developmental series; *Chrysocelis* with one-celled sessile teliospores, *Maravalia* with one-celled pedicellate teliospores and *Chrysocyclus* with two-celled, pedicellate teliospores. It should also be noted that a number of genera with similar teliospores form a parallel series in which the teliospores instead of arising singly from a compact hymenium, are produced in groups from laterally free basal cells. In this series are *Chaconia*, *Olivea* and *Desmotelium* with one-celled,

sessile teliospores, and *Allopuccinia* with two-celled pedicellate teliospores. It is believed that this arrangement best indicates the relationship of these genera.

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The aim of this Index is to include all current botanical literature written by Americans, published in America, or based upon American material; the word America being used in the broadest sense.

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Growth of Excised Tomato Roots in a Synthetic Solution

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(WITH TWO FIGURES)

The authors have previously reported (3, 4, 5) that a solution of mineral salts, cane sugar and thiamin (or the vitamin thiazole, 4-methyl-5β-hydroyethyl thiazole) appeared adequate for unlimited growth of excised tomato roots. At the time of the previous report the excised roots had been grown through 12 successive passages extending over a period of one year in a solution of mineral salts, pure cane sugar and thiamin and through seven successive passages extending over 7 months in a solution of mineral salts, cane sugar and thiazole. These roots have been kept in cultivation and those in the thiamin solutions are now in their 29th passage while those in the thiazole solutions are now in their 23rd passage. Since they are still growing with no evidence of a progressive diminution in growth or the development of abnormalities it would appear that these solutions are adequate for unlimited growth. Because of the long period of time through which the cultures have been maintained it seems desirable to record the results and to make some comments on them.

The clones of excised roots used in these experiments came originally from the germinated seeds of a pink fruited variety of tomato from Mexico, Ajo de Verrado, *No. 580*. Excised tips from the seedling roots were placed in White's solution (8), Sept. 29, 1935. After 13 passages in this solution subcultures were started Oct. 21 and 22, 1936 in a solution of minerals, cane sugar and thiamin. The subcultures in the thiazole solutions were begun Apr. 11, 1937 after 18 passages in a solution of minerals, sugar and yeast.

The excised roots were grown individually in 40 or 50 ml. of solution in 125 ml. Erlenmeyer flasks of Pyrex glass. The mineral salts were of chemically pure grade and the cane sugar was Pfanstiehl's chemically pure sucrose. The thiamin was Merck's synthetic. Two samples of thiazole

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have been used both furnished through the courtesy of Merck and Company. The first sample was dark in color and obviously impure, the second

TABLE 1

Growth of excised tomato roots in solutions of minerals, pure cane sugar and thiamin through 25 successive passages.

DATE	PASSAGE	NO. ROOTS WEIGHED	DRY WT. PER ROOT MG.	RANGE DRY WT. MG.	SOLUTION
1936					
Oct. 21, 22	14	8	4.5	0.8– 7.3	Wh
Nov. 24	15	7	7.1	2.7–17.1	Wh
Dec. 26, 27	16	5	4.6	1.6– 5.5	Wh
1937					
Jan. 30, 31	17	7	4.0	1.4– 5.6	Wh
March 5, 6	18	7	4.4	0.9–10.4	Wh
Apr. 6	19	9	7.5	2.6–23.1	Wh
May 8	20	14	11.5	1.9–26.7	Wh+B and Zn
June 9	21	6	16.5	10.7–25.4	Wh+B and Zn
July 16	22	6	7.5	5.2– 8.2	Wh+B and Zn
Aug. 23	23	7	5.6	0.4– 9.6	Wh+B and Zn
Sept. 27	24	5	3.0	2.1– 5.4	Wh+B and Zn
Oct. 19	25	4	8.3	6.0–11.2	Wh+B and Zn
Nov. 15	26	4	7.3	0.6–13.2	Wh+B and Zn
Dec. 14	27	4	1.6	1.1– 2.0	Wh+B and Zn
Dec. 14	27	6	9.9	4.0–19.8	Pf+B and Zn
1938					
Jan. 30	28	9	1.1	0.2– 5.2	Pf+$\frac{1}{2}$B and Zn
Mar. 3	28	9	0.8	0.2– 2.6	Wh+$\frac{1}{2}$B and Zn
Mar. 17	29	2	1.2	0.4– 2.0	Wh+$\frac{1}{2}$B and Zn
Apr. 12	30	3	0.1	0.1	Wh+$\frac{1}{2}$B and Zn
Apr. 12	30	5	0.8	0.1– 2.7	Pf+$\frac{1}{2}$B and Zn
May 16	31	4	3.2	0.1–12.3	Pf+$\frac{1}{2}$B and Zn
May 16	31	4	0.2	0.1– 0.3	Wh+$\frac{1}{2}$B and Zn
May 16	31	5	0.5	0.1– 1.2	Wh+Sol Z $\frac{1}{2}$
June 14	32	4	3.8	2.1– 8.2	Pf
July 12	33	9	9.9	6.3–16.8	Pf
Aug. 3	34	10	5.5	4.0– 6.8	Pf
Sept. 15	34	4	3.3	2.7– 4.3	Pf
Aug. 25	35	11	4.6	3.1– 8.6	Pf
Oct. 18	35	5	3.1	2.6– 3.6	Pf
Sept. 15	36	3	2.7	2.3– 2.6	Pf
Oct. 18	37	10	3.6	3.0– 5.0	Pf
Oct. 18	37	5	4.6	3.9– 5.6	Pf+$\frac{1}{2}$B and Zn
Nov. 19	38	7	5.7	3.3–10.1	Pf

was a specially pure sample furnished at our request. No great difference was noted in the effects of the two samples of thiazole. Thiamin and thiazole were added at the rate of 10 γ per flask. Solutions were steam steri-

lized under 10 or 15 lbs. pressure and the roots were grown in diffuse light at temperatures ranging from 20°C or somewhat less to a maximum of about 25°C.

Several mineral solutions were used. These included White's mineral solution, a modified Pfeffer's solution similar to that originally used by

TABLE 2

Growth of excised tomato roots in solutions of minerals, pure cane sugar and thiazole through 19 successive passages.

DATE	PASSAGE	NO. ROOTS WEIGHED	DRY WT. PER ROOT MG.	RANGE DRY WT. MG.	SOLUTION
1937					
Apr. 11	19	4	3.6	1.2– 8.2	Wh
May 8	20	4	13.7		Wh+B and Zn
June 9	21	2	24.6	23.8–25.5	Wh+B and Zn
July 16	22	2	12.9	11.7–14.1	Wh+B and Zn
Aug. 25	23	4	17.3	13.7–21.8	Wh+B and Zn
Sept. 27	24	4	23.1	14.3–32.9	Wh+B and Zn
Oct. 19	25	6	11.9	8.1–14.5	Wh+B and Zn
Nov. 15	26	7	12.6	0.4–28.9	Wh+B and Zn
1938					
Jan. 10	27	6	27.2	6.7–33.2	Pf+B and Zn
Jan. 10	27	3	19.8	13.2–25.0	Wh+B and Zn
Mar. 3	28	9	13.1	1.7–61.0	Wh+B and Zn
Apr. 12	29	8	12.0	0.8–25.0	Wh+½B and Zn
May 16	30	4	13.4	2.5–24.3	Wh+½B and Zn
June 14	31	2	13.6	11.0–16.3	Wh+½B and Zn
July 12	32	9	8.2	1.1–10.6	Wh
Aug. 3	33	10	8.4	4.9–14.5	Pf
Aug. 25	34	9	8.7	5.7–14.3	Pf
Sept. 15	35 Th_1	7	4.5	3.1– 6.3	Pf
Sept. 15	35 Th_2	7	4.0	2.6– 6.6	Pf
Sept. 15	35 Th_1	5	5.5	2.6– 9.1	Wh+½B and Zn
Sept. 15	35 Th_2	4	5.2	3.8– 6.7	Wh+½B and Zn
Oct. 18	36 Th_1	8	8.8	6.7–11.6	Pf
Oct. 18	36 Th_2	10	7.9	4.2–10.5	Pf
Oct. 18	36 Th_1	5	7.7	4.4–10.3	Pf+½B and Zn
Oct. 18	36 Th_2	5	9.1	7.1–11.9	Pf+½B and Zn
Nov. 19	37	3[1]	2.9	1.6– 4.1	Pf

[1] 4 of the best roots in this passage were used for inoculum.

Robbins (2) and the same solutions supplemented with 0.1 ppm B and 0.1 ppm Zn or 0.05 ppm B and 0.05 ppm Zn or an A to Z mixture (5) at one half strength. White's mineral solution contained per liter of distilled water $Ca(NO_3)_2$, 0.142 g.; $MgSO_4 \cdot 7H_2O$, 0.073 g.; KNO_3, 0.081 g.; KCl, 0.065 g., KH_2PO_4, 0.012 g.; $Fe_2(SO_4)_3$, 0.0024 g. The modified Pfeffer's

solution contained per liter $Ca(NO_3)_2$, 0.333 g.; $MgSO_4 \cdot 7H_2O$, 0.063 g.; KNO_3, 0.063 g.; KCl, 0.042 g.; KH_2PO_4 0.06 g.; $Fe_2(SO_4)_3$, 0.0025 g.

The growth in solutions containing thiamin is given in Table 1 and that in solutions containing thiazole in Table 2. The first column gives the date of addition of inoculum to the solutions; the second, the number of the passage since the seedling root was severed; the third, the number of roots weighed; the fourth, the average dry weight per root; the fifth, the range in the dry weights of individual roots and the last column, the special medium used. In the last column White's mineral solution is indicated by Wh, the modified Pfeffer's solution by Pf, 0.1 ppm B and 0.1 ppm Zn are indicated by B and Zn, 0.05 ppm Zn by $\frac{1}{2}$B and Zn and the A to Z mixture by Sol Z$\frac{1}{2}$. The first sample of thiazole is indicated by Th_1 and the second by Th_2.

As a rule the roots were grown for two months before dry weights were determined though on occasion they were grown for 2$\frac{1}{2}$, 3 or even 4 months. There seemed to be little relation between the final dry weights and the length of the growth period; some of the heaviest roots grew but two months. Other factors were evidently more important than time in determining total growth.

The growth in passages 28, 29, 30 and 31 in the thiamin solution was slight and we assumed that this might indicate that a solution supplemented with thiamin alone was not adequate for continued growth. However, the roots returned to more nearly normal weights in passages from 32 to 38. Whether the poor growth in passages 28 to 31 was caused by temperature variations, differences in the mineral salts used or some other factor is uncertain. The minerals might be thought to be concerned because of the poorer results in White's mineral solution than in Pfeffer's solution (see passages 28, 30 and 31).

That the decreased growth in passages 28, 29, 30 and 31 was not an indication of "running out" is shown in figures 1 and 2. These figures show the fragment used for inoculum and the root which grew from it in the 21st successive passage in a solution of minerals, sugar and thiamin and the original inoculum and resulting root in the 15th successive passage in a solution of minerals, sugar and thiazole. The fuzziness of the roots in these photographs is in part due to the presence of root hairs.

The largest root in the thiamin solutions weighed 26.7 mg. (passage 20) and the highest average weight was 16.5 mg. (passage 21). In general the variability of the roots grown in the thiamin solutions was greater than those in the thiazole solutions.

The largest root in the thiazole solutions (61 mg.) was in passage 28. These roots grew 4 months which may account for the large size. In pas-

sage 24 the period of growth was 2 months and the largest root weighed 32.9 mg. The best average weight was 27.2 mg. in passage 27. Up to passage 31 the average dry weights were higher than those of later passages. This is in part accounted for by longer periods of growth in the earlier passages where many of the roots grew for 3 or 4 months before weights were taken. From passage 32 on the dry weights were determined after 2

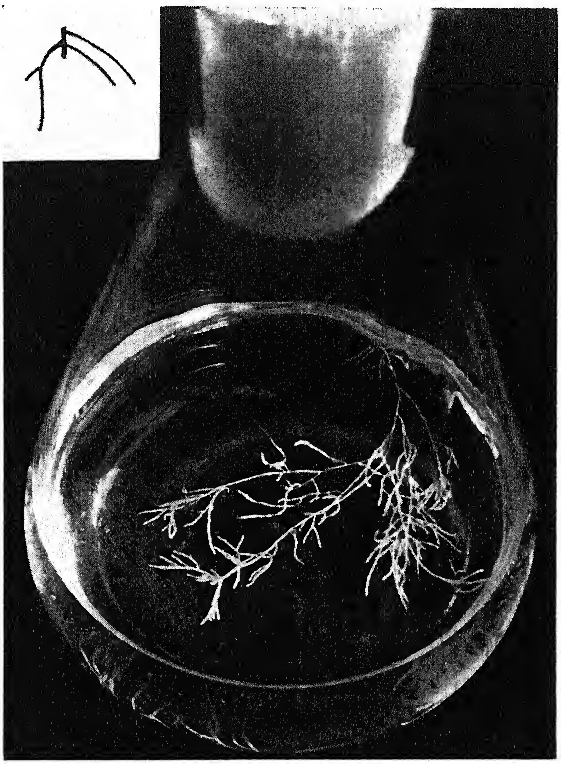

Fig. 1. Photograph of excised root of tomato grown in Pfeffer's solution plus 2 per cent cane sugar and 10 γ of thiamin in Passage 34, the 21st successive passage in a solution of minerals, sugar and thiamin. The root fragment from which this root grew is shown by the drawing in the upper left hand corner. Age 7 weeks.

months growth. However, in passages 20, 23 and 24 the period of growth was 2 months; factors other than time are evidently important.

In general we have found the modified Pfeffer's solution preferable to White's mineral solution. Some of our results showed that the addition of boron and zinc was beneficial but later experiments made such a conclusion doubtful, especially when the boron and zinc were added to White's mineral solution. One of the major difficulties in such experiments is to

secure chemicals of uniform purity (or impurity) and since it was necessary to use different lots of mineral salts during the course of these experiments some of the variation in the results of successive experiments might have been caused by differences in the impurities present in different lots of mineral salts.

Fig. 2. Photograph of excised root of tomato grown in Pfeffer's solution plus 2 per cent cane sugar and 10 γ of vitamin thiazole in Passage 33, the 15th successive passage in a solution of minerals, sugar and thiazole. The root fragment from which this root grew is shown by the drawing in the upper left hand corner. Age 7 weeks.

No facilities for maintaining a constant temperature were available and variations in temperature also account in part for differences in growth in successive passages.

Furthermore, the best roots in each passage were used as sources of inoculum and were not included in the dry weights; the dry weights in all instances were, therefore, less than the maximum.

The roots grown in these solutions as a rule developed many branches of about equal size (see figures 1 and 2); that is, except occasionally in the

early stages of growth there was no dominating main root tip. Root hairs were freely produced and an occasional root which remained undisturbed became fastened firmly to the bottom of the flask by the root hairs. This was somewhat surprising in view of the smooth unscratched surface to which they became attached and was interpreted to mean that the walls of the root hairs were sufficiently gelatinous when first formed to stick to the glass.

One of the interesting observations from these data is that the growth in the solutions supplemented with thiazole was generally superior to that in solutions supplemented with thiamin. This was unexpected as we believe that the effective agent is thiamin, the tomato roots in the solutions supplemented with thiazole form vitamin pyrimidine (5) and we have assumed that thiamin is made by the tomato root from the two intermediates. It is possible that with a considerable excess of thiamin, as occurs in the solutions used in these experiments, sufficient pyrimidine was present to be injurious.

Another conclusion to be drawn from all these experiments is that amino acids are not essential for the growth of excised roots as might be concluded from the papers by Bonner and Addicott (1) and by White (9). The sole source of nitrogen available to these excised roots throughout the experiments was in the form of nitrates. It is clear from these results that this strain of tomato roots was capable of synthesizing its proteins from nitrates.

Although it would appear from these results that unlimited growth of this strain of tomato roots is possible in a solution of minerals, sugar and thiamin or in a solution of minerals, sugar and thiazole there is of course a possibility that the cane sugar used, in spite of its high purity, contained traces of another growth substance. In addition even though no growth occurs without thiamin or thiazole the rate of growth in the presence of these supplements is slow. The slowness of growth is because of the limited ability of the roots to synthesize adequate amounts of a second growth substance needed in their development. This second growth substance is vitamin B_6 (6, 7).

It should not be concluded from these results that the excised roots of other kinds of plants must be supplied with thiamin or thiazole and vitamin B_6 for successful growth in liquid cultures. Many growth substances are probably concerned in the development of a root. The roots of one kind of plant, the tomato for example, may be deficient in thiamin (or thiazole) and vitamine B_6. Those of another kind of plant may synthesize adequate amounts of one or both of these substances but lack the ability to make others. It is necessary, however, to make sure of our understand-

ing of the requirements of one root in order that the results may be intelligently applied to those of others.

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The Microfibrillar and Microcapillary Structure of the Cell Wall[1]

I. W. Bailey

(WITH 11 FIGURES)

A detailed microscopic examination of different types of cells in various tissues and in a wide range of both gymnosperms and angiosperms reveals much diversity in the visible structure of cell walls. The commonest and most salient types of structural patterns[2] in secondary walls are (1) concentric layering or lamellation, (2) radial and ramifying lamellations, and (3) radio-concentric patterns, complex combinations of the two preceding types. The structural patterns of different cell walls fluctuate in texture from such as are relatively coarse and clearly visible under high magnifications to others that are invisible except in swollen preparations. When walls of the former type are carefully and gradually expanded, finer and finer details of structure become visible under the microscope without serious modification or distortion of the original structural design (Bailey and Kerr, 1935; Kerr, 1937; Bailey, 1938). In all cases, regardless of variations in texture, the cellulose resolves itself ultimately into a porous matrix composed of tenuous coalesced fibrils. In other words, the diverse structural patterns are due to varying densities or porosities in different parts of the cellulosic matrix (figs. 1 and 3). In the denser parts, the volume of the interfibrillar capillary spaces is reduced, and the fibrils are more numerous per unit area and are more extensively coalesced. Conversely, in the more porous parts, the volume of the capillary spaces is increased, and the fibrils are less closely approximated.

The specific and characteristic structural patterns seen in cell walls of the higher plants are not artifacts induced by swelling, *since they frequently are visible in unswollen walls.* Nor are they due to secondary changes or rearrangements occurring subsequent to the formation of the cell walls, since identical patterns are clearly visible in the developing walls of growing and differentiating cells. During the earlier stages of the formation of both primary and secondary walls,[3] it is possible to demonstrate, visually, that the cellulose is deposited in the form of coalescing fibrils of varying diameters and orientations (fig. 7). Furthermore, as Kerr (1937) and Anderson and Kerr (1938) have so clearly shown, the formation of alternat-

[1] Presented before Section G of the American Association for the Advancement of Science at Richmond, Virginia, Dec. 28, 1938.

[2] As seen in sections cut at right angles to the long axis of a cell.

[3] For a discussion of the distinction between primary and secondary walls see Kerr and Bailey (1934).

ing concentric lamellae of varying porosity is due, in the cotton hair, to fluctuating environmental factors; e.g., more porous lamellae are formed at night and denser ones during the daytime. Thus, the hairs of different cotton plants—grown during the same period of varying environmental influences—may exhibit identical patterns of lamellae, and it is possible to cross-date the *daily* growth rings, much as the *annual* rings in stems of western yellow pine may be cross-dated.

In the case of heavily lignified walls, the lignin may be removed, leaving a coherent matrix of cellulose; or conversely, the cellulose may be extracted, leaving a coherent residue of lignin (Bailey and Kerr, 1935; Bailey, 1938). The two types of residues are remarkably similar and are, in fact, positive and negative images of the same structural pattern (figs. 1 and 2). The pattern of the lignin residue may be interpolated within the porosities of the cellulosic matrix and *vice versa*. This demonstrates not only that the lignin is deposited within the interfibrillar capillary spaces of the cellulosic matrix, but also that the elongated interstices of the cellulose are intercommunicating (figs. 4 and 5). It is evident, accordingly, that in dealing with cell walls, we are concerned with two continuous interpenetrating systems, one of coalesced fibrils of cellulose and the other of interconnecting capillary spaces. The capillary system may be filled with water or may contain varying percentages of lignin, polyuronides, polyoses, tannins, phlobaphenes, terpenes, resins, and other complex organic compounds.

It should be noted in this connection, however, that not all the visible

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Explanation of Figs. 1-5

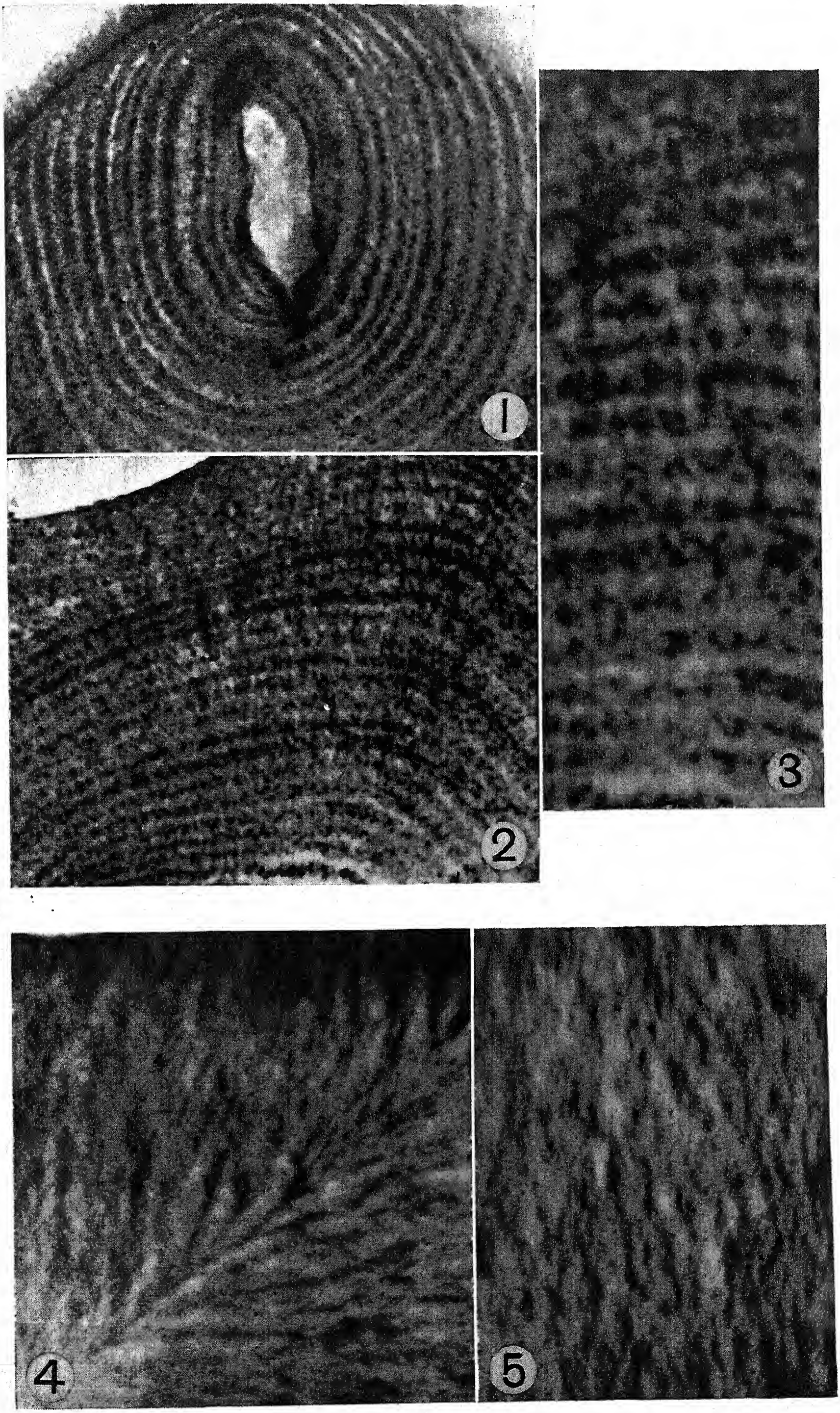
Fig. 1. Expanded transverse section of a concentrically lamellated secondary wall. The microfibrils of cellulose (dark) and the microcapillaries (light) are seen in cross section. In the denser lamellae, the microfibrils are more closely aggregated and more extensively coalesced than in the lighter, more porous lamellae. Total enlargement. ×7500.

Fig. 2. Coherent lignin residue from a structurally similar type of secondary wall. The microfibrils of lignin, which filled the microcapillaries illustrated in fig.1, are dark; whereas the porosities left by the removal of the cellulose are light. Figs. 1 and 2 are obviously positive and negative images of the same structural pattern, and the lignin residue may be interpolated within the porosities of the celllulosic matrix and vice versa. Total magnification. ×9000.

Fig. 3. Illustrates a portion of either fig. 1 or fig. 2 very highly magnified. The more or less closely aggregated fibrils are dark, the porosities are light. Total magnification. ×25,000.

Fig. 4. Expanded transverse section of a secondary wall, having a radio-ramifying structural pattern. Total magnification. ×5850.

Fig. 5. Expanded longitudinal section of such a wall, showing the coalesced microfibrils. Total enlargement. ×5850.



Figs. 1–5

structures of cell walls are due solely to variations in density or porosity of the cellulosic matrix. More or less conspicuous concentricities may be produced, at times, by varying amounts of lignin or of other substances that are deposited in different parts of the cell walls. Furthermore, actual discontinuities, due to the presence of non-cellulosic layers or lamellae, occur characteristically in the walls of certain specific types of cells (Bailey and Kerr, 1935),—e.g., tracheids of "Rotholz," so-called gelatinous fibers, sclereids, etc. In addition, most of the thicker types of walls exhibit concentric layers of varying indexes of refraction that are due primarily to different orientations of the microfibrils in successively-formed layers of the cell wall (Bailey and Vestal, 1937a). In other words, the microfibrils and the elongated microcapillaries may be oriented parallel to the long axis of the cell, at right angles to this axis or helically in relation to it (fig. 8).

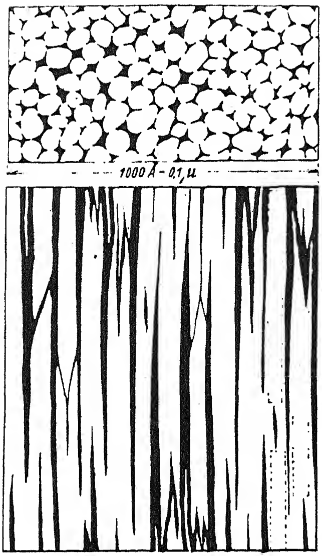


Fig. 6. Frey-Wyssling's conception of the submicroscopic structure of cellulose as viewed in transverse and longitudinal sections. The coalesced micelles (light) are separated laterally by intermicellar spaces (dark).

The evidence summarized in the preceding paragraphs indicates that, in the field of microscopically visible structures, cellulose is composed of a continuous system of coalesced microfibrils which is perforated by a continuous system of intercommunicating microcapillaries. It is of interest to compare the visible structure of cellulose with pictures of its structure postulated by workers in the submicroscopic field. For many years following the publication of Nägeli's micellar theory, the micelles or crystallites of cellulose were considered to be discrete entities separated on all sides by intermicellar spaces. Evidence obtained largely by X-ray analyses was interpreted as indicating that these micelles are composed of aggregations of chain molecules oriented parallel to one another with specific and characteristic spacings between the individual chains of the aggregation. More recently, Frey-Wyssling (1936, 1938), in order to harmonize the conflicting evidence from various fields of physical and chemical research, has profoundly modified this classical conception. As indicated in fig. 6, he now regards cellulose as a continuous matrix of overlapping chain-molecules which is perforated by a continuous system of intermicellar capillaries. In other words, micelles are no longer to be regarded

as discrete crystallites, but merely as anastomosing parts of a coherent porous matrix. There is much that can be said in favor of such a view, since it allows for chain-molecules of greater length, for the coherence of purified cellulose, and for various optical, physical, and chemical properties of cell walls in general. It should be recognized, however, that according to this modification of Nägeli's hypothesis, the crystallite loses its individuality and possibly should no longer be designated as a micelle.

Frey-Wyssling's modified conception of the submicroscopic structure of cellulose so closely resembles the finer visible structure of the cell wall that the question arises: Are there two distinct sizes of fibrils and of capillaries, or are there series of these structures that grade down in size to "micelles" and "intermicellar" spaces? Reliable factual data are not available, at present, for conclusively answering this question; but it is desirable to discuss certain aspects of the problem which may be significant in its clarification. A number of investigators maintain that lamellae are composed of a single layer of fibrils, and that the diameter of the fibrils and lamellae is constant. It is difficult, however, to homologize the constants obtained by different workers. For example, the diameter of fibrils is considered by some to be 4000 Å, by others 11,000 Å, and by others as much as 30,000–40,000 Å. That such *macrofibrils* are heterogeneous is indicated by their particle double refraction, by their dichroism, and by other optical and physical evidence. Furthermore, cellulosic primary walls frequently are less than one micron in thickness and obviously cannot be constituted of particles or fibrils 11,000 Å in diameter.

The approximate diameters of the finest lamellae and microfibrils that are visible in swollen walls may be determined by the following procedure.[4]

[4] It should be emphasized, in this connection, that if the expansion of the wall is not accurately controlled, the original structural pattern will be seriously modified or destroyed, and various artifacts may be produced. Thus, it is essential to avoid (1) degrading the cellulose by oxidation or hydrolysis and dissecting the wall into fusiform bodies and other small fragments before swelling occurs; (2) dissociating the aggregated microfibrils by excessive or unduly rapid expansion and dissecting them into minute particles; and (3) precipitating dispersed cellulose in the form of granules. Where the process of swelling is skillfully controlled, the highly specific and characteristic structural pattern—whether concentric, radial, ramifying, or radio-concentric of a particular type of cell wall is retained and expanded. This is true regardless of the plane of sectioning of the cell, whether transverse, longitudinal, or diagonal. A small fragment of the wall exhibits its own characteristic part of the particular structural pattern from which it was removed. The argument that the structural patterns are artifacts due to pressure during swelling, is thoroughly invalidated by the fact that the characteristic patterns frequently are visible in unswollen sections and persist during swelling, regardless of whether the sections are pressed under a cover glass or not.

The diameter of a wall in its unswollen condition is accurately measured. The wall is then expanded, and the number of its constituent lamellae is counted. If the wall is X units in diameter and is composed of Y lamellae, the average diameter of the lamellae in the unexpanded wall must be X/Y. By the use of this procedure it is possible to determine that the width of the finest lamellae is 500 Å or less. The diameter of the microfibrils also is 500 Å or less, since the narrowest lamellae are composed of a single layer of fibrils and the wider ones of more than one layer. The visible expanded microfibrils fluctuate somewhat in size, but it is not possible, at present, to determine whether this is due to inequalities in swelling or solely to inherent differences in diameter of the unexpanded microfibrils. Furthermore, since the microfibrils are not visible in their unswollen state, it is not possible to study their optical anisotrophy or their dichroism except in a condition where the spacing of their constituent chain-molecules may have been modified. The microcapillaries commonly are less than 500 Å in diameter, but there are no reliable data available for determining their exact dimensions or for demonstrating whether they are of constant or of fluctuating cross-sectional area. Measurements obtained from lignin residues are unreliable, since the microcapillaries of the cellulosic matrix may have been enlarged by the infiltrating lignin; there is said to be some swelling of walls during lignification. Similarly, there is a considerable element of uncertainty in attempting to compute the diameters of the microcapillaries by measuring the diameters of crystals that may be deposited within them (Frey-Wyssling, 1937a; 1937b). For, on the one hand, the diameter of the crystals may be less than that of the microcapillaries, and, on the other hand, it may be greater; viz., where the crystals enlarge the microcapillaries by crowding the microfibrils apart (fig. 8). That the latter phenomenon actually occurs may be observed in cases where the crystals or crystal aggregates enlarge to visible dimensions (Bailey and Vestal, 1937a; Frey-Wyssling, 1937b). Nor is it safe to assume that the so-called micelle is of constant dimensions. The much quoted values of 500–750 × 50–60 Å were obtained from X-ray analyses of a specific type of cell wall,—i.e., that of ramie fibers (Hengstenberg and Mark, 1928). Even if the calculations were based upon thoroughly reliable assumptions, which is by no means certain, such measurements cannot be accepted as constants until a number of diverse types of cell walls have been analyzed.

In view of such facts as these, the present status of available information regarding the structure of the cellulosic wall of the higher plants may be summarized briefly as follows:

Chemical and physical research indicates that cellulose is composed fundamentally of more or less elongated chains of anhydrous glucose

residues. These chain-molecules tend to occur in aggregations within which they are arranged parallel to one another with characteristic spacings between the individual chains. In addition, there is evidence which suggests that the aggregations of chain-molecules are not discrete and separate entities, but that they are parts of a continuous system, which is held together by overlapping chain-molecules and is perforated by a continuous system of "intermicellar" spaces.

Similarly, in the field of microscopically visible structures, the cellulosic matrix appears to be a continuous system composed of coalesced microfibrils which grade down to 500 Å or less in diameter (Freudenberg, 1932; Bailey, 1938). The matrix is perforated by a continuous system of interconnected microcapillary spaces which may be filled with water or with lignin and a wide variety of other organic compounds. The visible structural patterns of both primary and secondary walls are due—except in certain specific types of cells—primarily (1) to variations in the density or porosity of the cellulosic matrix; (2) to different types or percentages of non-cellulosic substances that are deposited within the microcapillaries; or (3) to changes in the orientation of the microfibrils and microcapillaries in successively-formed layers of the cell wall.

Although the evidence from both the microscopic and the sub-microscopic fields of research indicates that the cellulosic matrix of cell walls is a continuous rather than a discontinuous system, there is a dearth of reliable information regarding structural details which may intervene between the unit cell and 500 Å. There appear to be no reliable data available, at present, for determining whether microfibrils are of constant or of fluctuating diameter, whether they are heterogeneous and composed of still finer coalescing fibrils, or whether they are constituted directly and solely of anastomosing "micelles"; similarly, whether there are two distinct sizes of capillary spaces, or whether the microcapillaries and the "intermicellar" spaces are connected by interstices of intermediate or transitional sizes. It is essential to clarify such uncertainties as these, since it is structures in this general field of magnitudes, 10–500 Å, that are likely to be of considerable significance, not only in the solution of various problems in the economic utilization of pulp and of cellulose and its derivatives, but also in the elucidation of a number of obscure physiological processes.

It should not be inferred from this, however, that many of the properties of cell walls can not be accounted for upon the basis of available data. For example, many of the conspicuous differences in the optical and mechanical properties of cell walls and wall layers are closely correlated with variations in the orientation of the microfibrils and microcapillaries. Walls

or layers composed of microfibrils which are oriented parallel to the long axis of the cell are isotropic in transverse sections and do not contract longitudinally in drying; whereas walls having transversely oriented microfibrils are strongly birefringent in cross sections and contract longitudinally in drying. Various intermediate conditions occur in walls whose microfibrils are oriented helically in relation to the long axis of the cell. Although the two types of physical anisotropy are due, fundamentally, to the arrangement of aggregates of chain-molecules, the microfibrils may be utilized as indicators, since the long axis of the chain-molecules and of the "micelles" is oriented parallel to that of the microfibrils.

It should be emphasized, in this connection, that there is a considerable element of uncertainty in attempting to account for the optical and other physical properties of specific types of cell walls solely upon the basis of putative "micellar" arrangements, without regard to the microfibrillar orientations. Thus, a wall may be isotropic in surface view, not because the "micelles" are randomly oriented throughout it, but because the microfibrils in its successively-formed layers are variously oriented. In other words, the chain-molecules and "micelles" have a preferred orientation—parallel to the long axis of the microfibrils—in each layer, but where the layers are of relatively uniform thickness the wall may exhibit isotropy in surface view. Furthermore, walls of this character may give a ring-type of X-ray diffraction pattern which is commonly interpreted as an indication of a truly random orientation of crystallites. It is such phenomena as these which have led to various misconceptions regarding the structure of primary walls and concerning changes that occur during their increase in surface area. In fact, in studying the growth and expansion of primary walls, attention may profitably be focused upon visible adjustments and rearrangements in the microfibrillar and microcapillary systems rather than solely upon postulated changes in the "micellar" system. The extinction angles of individual macrofibrils in monochromatic polarized light usually are clearly and sharply defined, whereas those of the cell wall as a whole may be vague and indefinite. The latter condition commonly is due, not to "scattering" or deviations in the alignment of adjacent "micelles," but rather to fluctuations in the orientation of the fibrils. The optical anisotropy of the fibrils of native cellulose appears to be *positive* in all cases, and the so-called positive and negative birefringences of cell walls is determined by the orientations of the fibrils in relation to the long axis of the cell. There is no reliable evidence, at present, to indicate that the structural framework of the plant cell wall ever is composed of randomly oriented cellulose. In all the various structural types of cells that I have

examined, the cellulose exhibits a preferred orientation in each of the tenuous, successively-formed parts of the cell wall.

The enzymatic hydrolysis of cellulosic walls (fig. 9), due to the activity of certain wood-destroying fungi, progresses along two predetermined sets of planes (Bailey and Vestal, 1937b), as does the acetylation of cellulose. One of these sets of planes is oriented parallel to the long axis of the microfibrils and *pari passu* of the microcapillaries, "micelles," and chain-molecules. The other is oriented at an angle of from 20–25 degrees to this axis. The latter set of planes of hydrolysis and of chemical reaction is not correlated with any visible structure of the cellulosic matrix, but it does correspond rather closely—as the computations[5] of my colleague, Professor Thimann, have shown—with certain spacings within the crystal-lattice of cellulose. These spacings are between the easily hydrolyzable ether-linkages of the cube-center and cube-side chains. They fluctuate around 14± Å, and form planes which interesect the long axis of the chain-molecules at angles of from 22°40′ to 25°04′. Although the submicroscopic and the visible planes are oriented at similar angles, it is not evident why the chemical reactions should progress along these specific planes. If it be assumed that the spacing between the ether-linkages is of the most favorable magnitude for the insertion and activities of enzyme molecules, it is not clear why the reactions due to acetylation or to hydrolysis by phosphoric or sulphuric acids—where smaller molecules are concerned should progress along the same planes. Nor is it evident why the enzymatic hydrolysis should progress so commonly along a single plane rather than in a zigzag manner, since at any specific ether-linkage, it would seem that hydrolysis might progress in various directions, either upward or downward, at angles of from 22–25 degrees. Therefore, the most that may be concluded, at present, is that there are specific predetermined planes of chemical reaction in native cellulose, certain of which are closely correlated with visible orientations in the cellulosic matrix and others which must be due solely to molecular configurations.

Similarly, in the case of mechanically-induced cracking of the cell wall, (figs. 10 and 11) there are predetermined planes of cleavage, certain of which may be correlated with visible weaknesses of the cellulosic matrix and others that are due to submicroscopic factors. One of these sets of planes of structural weakness is oriented parallel to the long axis of the microcapillaries and microfibrils and is much accentuated in cell walls

[5] These computations were made in 1937, but were not published, owing to uncertainties in their interpretation. They are in substantial agreement, however, with those recently published by Frey-Wyssling (1938).

having concentric or radial lamellae of strikingly different porosities or densities. Such walls tend to split concentrically, radio-longitudinally, or radio-helically, even in ordinary drying; whereas walls of more uniform texture or of ramifying patterns do not. Failures, due to excessive compression, tension, torsion, etc., are of three distinct types: (1) oriented parallel to the long axis of the microfibrils and microcapillaries, (2) oriented approximately at right angles to this axis, or (3) of inconstant orientations. The so-called slip-planes, which have attracted so much attention in the literature, usually are discussed and figured as seen in sectional views of relatively thick secondary walls. The inclinations of these planes of buckling fluctuate over a range of nearly 90 degrees and are determined largely by the orientation of stresses and strains operative in their production. On the contrary, in surface views of cell walls, or of their constituent layers, the planes of buckling frequently are oriented nearly at right angles to the long axis of the microfibrils and microcapillaries. Since there are no visible structural weaknesses in this predetermined plane of buckling, it must be due to submicroscopic factors.

It should be emphasized in conclusion that, owing to the presence of predetermined planes of cleavage and of chemical reaction, the continuous cellulosic system of the cell wall may be dissected into fragments of varying forms and sizes,—e.g., dermatosomes, ellipsoid particles, fusiform bodies, macrofibrils, lamellae, layers, etc. The shape and the dimensions of such fragments are dependent upon the type of wall under consideration and upon the specific mechanical and chemical treatments to which it is subjected.

Explanation of Figs. 7-11

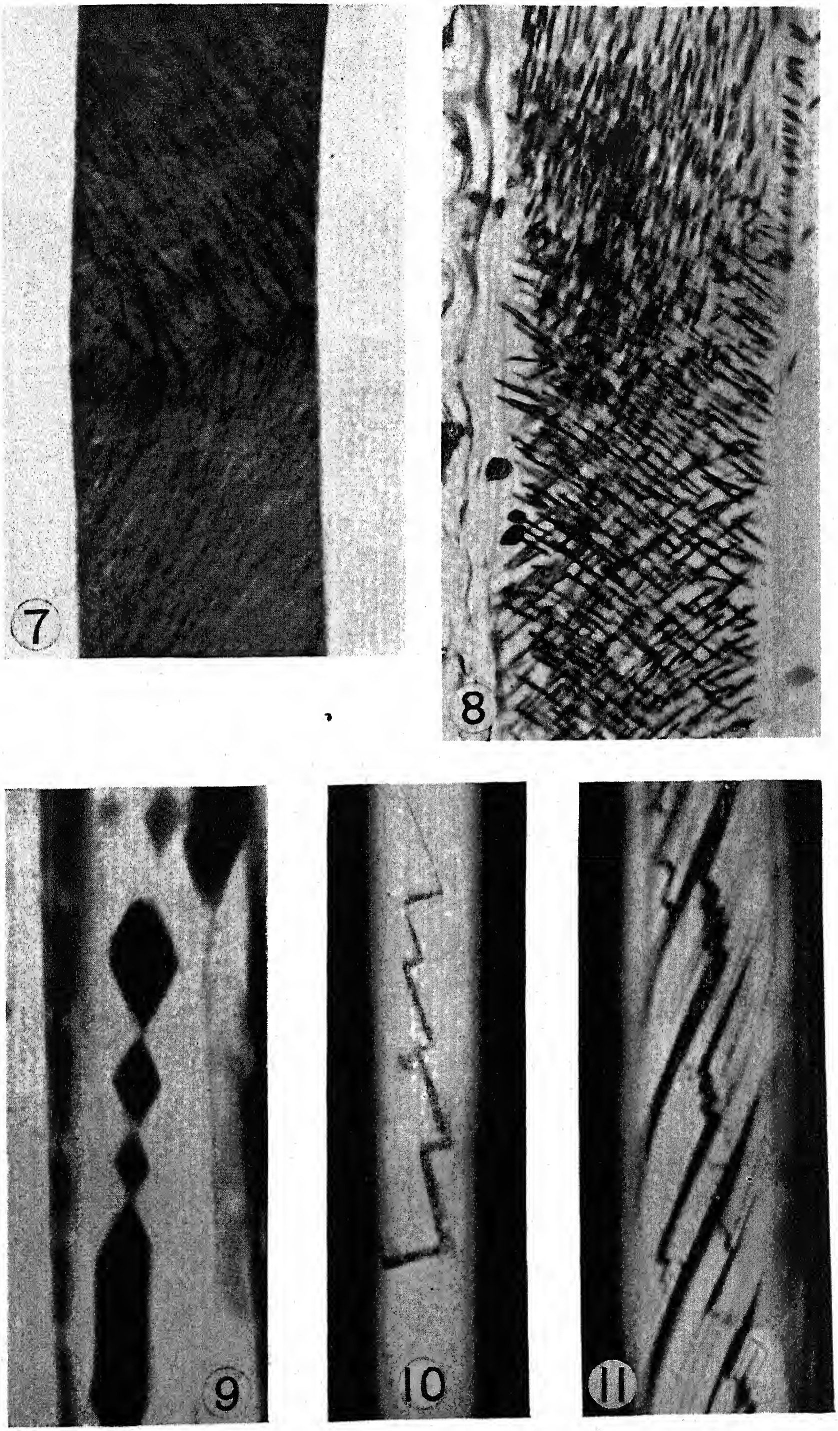
Fig. 7. Early stage in the formation of the secondary wall of cotton, showing coalescing fibrils and a "reversal" in their orientation. ×900. Photo by Dr. Thomas Kerr.

Fig. 8. Longitudinal section through parts of the secondary walls of two adjacent tracheids, showing three orientations of visible crystals of iodine. The crystals may be utilized in determining the orientation of the microcapillaries in the three layers of secondary wall, but they have enlarged the microcapillaries by crowding the microfibrils apart. ×900.

Fig. 9. Longitudinal section of a secondary wall, photographed in polarized light between crossed Nicols, showing cavities produced by wood-destroying fungus. There are two sets of planes of enzymatic hydrolysis, one oriented parallel to the long axis of the microfibrils and the other at an angle of from 20–25° to this axis. ×990.

Fig. 10. Longitudinal section of a secondary wall, photographed in polarized light between crossed Nicols, showing two planes of mechanical cleavage. ×700.

Fig. 11. The same. ×700.



Figs. 7–11

SUMMARY AND CONCLUSIONS

The cellulosic matrix, of the cell walls of the higher plants, appears to be a continuous rather than a discontinuous system. Physical and chemical data suggest that it is composed, in the submicroscopic field, of aggregations of chain-molecules that are held together by overlapping chain-molecules. In the microscopically visible field, it is constituted of coalesced microfibrils. In both fields of magnitude, the continuous cellulosic system is perforated by a continuous system of interconnecting capillary spaces.

The diverse structural patterns of varying texture, that are visible in both unswollen and expanded cell walls, are due in most cases (1) to variations in the number and proximity of the microfibrils and microcapillaries —i.e., variations in density or porosity—in different parts of the cellulosic matrix; (2) to different types or percentages of non-cellulosic substances that are deposited within the microcapillaries; or (3) to changes in the orientation of the microfibrils and microcapillaries in successively-formed layers of the cell walls.

The long axis of the chain-molecules and of the anastomosing "micelles" is oriented parallel to the long axis of the fibrils which exhibit positive anisotropy and sharply defined extinction angles in monochromatic polarized light. The vague and indefinite extinction angles of certain types of cell walls are due, apparently, not to deviations in the orientation of adjacent "micelles," but to fluctuations in the orientation of the fibrils. Similarly, isotropy in the surface view of cell walls and ring-types of X-ray diffraction patterns are not indicative, necessarily, of truly random orientation. The phenomena appear to be due to the fact that, although the cellulose has a preferred orientation in each set of microfibrils, the arrangement of the microfibrils fluctuates in the successively-formed tenuous lamellae of the wall. In fact, there is no reliable evidence, at present, to indicate that the structural framework of the cell wall ever is composed of randomly oriented cellulose.

There are predetermined planes of chemical reaction and of mechanical cleavage in the cell wall. Certain of these are closely correlated with visible structures, whereas others must be due to molecular configurations. Although the cellulosic matrix is a continuous system, it may be dissected into fragments of varying shapes and sizes by drastic mechanical and chemical treatments.

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Pollen Analysis of a Bog near Spokane, Washington

Henry P. Hansen

(with one figure)

Postglacial forest succession in eastern Washington has been interpreted from pollen analysis of a bog about twenty miles northeast of Spokane. The bog lies at an elevation of 2100 feet, in T. 26 N., R. 45 E., Sect. 11 on the Spokane Quadrangle. The peat deposit, which covers about a section in area, is situated at the southern end of Newman Lake. Much of it is now used for growing wheat. The depth of the peat is 7.3 meters, and it is uniform in thickness over much of its area. A layer of volcanic ash occurs from the 4.7 to the 4.4 meter levels, a thickness considerable greater than that usually found in bogs of the Pacific Northwest (Hansen 1938, Rigg 1938). This may have been due to the heavy rains which generally follow volcanic eruptions, transporting the ash into the lake.

The lower meter of peat consists of a gray-brown sedimentary type overlaying sand. This grades upward into fibrous sedge peat, with the ash above separated by a sharp line of demarcation. Immediately above the ash again occurs sedimentary peat which indicates inundation of the bog at this time, suggesting that abnormally heavy rains followed the volcanic eruption. The sedimentary peat grades into fibrous sedge peat toward the surface.

Near the shore of the lake exists a floating plant hydrosere followed on land by zones of cattail, bulrush, sedge, and rush.

The peat samples were taken with a Hiller borer at half-meter intervals, at a distance of about 500 feet inland from the shore of the lake. The peat is fresh and unoxidized throughout its entire depth.

For study, the peat was deflocculated by boiling in a weak solution of potassium hydrate, washed several times, centrifuged, stained with gentian violet, and mounted in glycerin jelly. Three hundred pollen grains were identified from each level.

AGE AND ORIGIN OF THE BOG

The bog and lake are situated near the mouth of a small tributary system which formerly drained into the Spokane River valley a few miles to the south. This area was covered by the Spokane glaciation, which has been correlated with the pre-Wisconsin by some geologists (Bretz 1923, Leverett 1917). Flint (1937) finds no evidence of pre-Wisconsin glaciation, and considers the so-called Spokane glacier in this part of Washington to be of Wisconsin age. During the recession of the ice, the Spokane River aggraded its valley with glaciofluviatile sediments and caused

blockades at the mouths of many of its tributaries (Flint 1936). This resulted in the ponding of Newman Lake basin and the subsequent development of the bog. Bogs in the driftless area of Wisconsin, situated in the valleys of tributaries of the Mississippi and Wisconsin Rivers, have a similar origin (Hansen 1933). Thus the bog came into existence at the close of the Wisconsin glaciation, and probably records the forest succession which has occurred in adjacent areas during most of post-Wisconsin time.

FORESTS IN ADJACENT AREAS

The bog lies within the timbered Arid Transition zone as defined by Merriam (1898). Spokane has a mean annual precipitation of about 18 inches. Forest-type maps show a western yellow pine (*Pinus ponderosa*) type covering much of the adjacent areas. The treeless Arid Transition zone exists a few miles to the south and west. At higher elevations to the north and east, yellow pine is replaced to some extent by more montane types, of which western white pine (*Pinus monticola*) is the commonest. Other species include Douglas fir (*Pseudotsuga mucronata*), western larch (*Larix occidentalis*), western hemlock (*Tsuga heterophylla*), white fir (*Abies grandis*), western red cedar (*Thuja plicata*), and lodgepole pine (*Pinus contorta*). The latter is also common on terraces along the Spokane River where it forms dense, pure stands. At still higher elevations on north exposures and damper sites, Englemann spruce (*Picea engelmanni*), mountain hemlock (*Tsuga mertensiana*), and subalpine fir (*Abies lasiocarpa*), are present.

FOREST SUCCESSION

The first forests to invade this area in postglacial time consisted of lodgepole and white pines, and western larch. These show pollen frequencies of 34, 15, and 23 per cent respectively, in the lowest level (fig. 1). The dominance of this forest is recorded to the 6 meter level, from which white pine and larch decrease rapidly and lodgepole pine less so. The pollen curves of these species correlate with their relative tolerance for shade, lodgepole being the most intolerant, followed by larch and white pine (Larsen 1930). Lodgepole is the first to decrease, while larch and white pine still increase, then larch begins to decrease while white pine still increases and finally decreases. No yellow pine pollen is recorded in the lower two levels, but it has frequencies of 2 and 5 per cent at the 6.5 and 6 meter levels.

The decrease of these pioneer forests and the sharp increases of grass, chenopods, and composites which are shown in the diagram, indicates the initiation of a warmer and dryer climate occurring during the deposition

of peat between the 5.5 and 4 meter levels. At the 5.5 and 5 meter levels grass pollen has frequencies of 38 and 25 per cent respectively. A heavy influx of grass during this period marks the extension of the treeless Arid Transition zone into areas near the bog. This life zone is at present characterized by grasses, including bunchgrass (*Agropyron spicatum*) and June grass (*Poa sandbergii*), and by the composite, balsam root (*Balsamorhiza sagittata*), in eastern Washington (Piper 1906). As increased dryness apparently continued the Upper Sonoran life zone became more widespread. Characteristic species of this zone include such composites as sagebrush (*Artemisia tridentata*) and rabbit brush (*Chrysothamnus nauseosus*), and the chenopods, hop sage (*Grayia spinosa*), greasewood (*Sarcobatus vermiculatus*), and saltbush (*Atriplex argentea*). The pollen count at the 4.5 meter level shows 15 per cent for the former and 16 per cent for the latter (fig. 1). The chenopods thrive under more saline conditions than the composites, but it would be difficult to say if and how salinity played any part at this time. It is to be noted that the volcanic eruption recorded by the ash, occurred near the close of grass-chenopod-composite dominance. The Upper Sonoran zone at present is confined chiefly to south-central Washington, but it extends up the Columbia and Spokane River valleys, and in the latter it reaches to within a distance of twenty-five miles west of Spokane (Piper 1906). It is likely that the flora of this zone formerly existed farther up the Spokane River Valley and was sufficiently close to be recorded by pollen in the bog.

The termination of the xerothermic period is marked by increases in larch, and yellow, white, and lodgepole pines. Larch assumes the more aggressive aspect with 20 per cent at 4 meters, but from this point it shows a constant decrease to the surface. Lodgepole pine steadily increases to 23 per cent at 2.5 meters, white pine to 23 per cent at 1 meter, and yellow pine increases sharply to 42 per cent at 2 meters. This period apparently was one of increasing coolness and moisture, with a mixed forest of these four species, and yellow pine assuming the dominant rôle. Other trees, indicated by low pollen percentages during this period, include western hemlock, Douglas fir, white fir, and Englemann spruce.

A final period, recorded from 2 meters to the surface, is marked by the existence of a western yellow pine climax, which has persisted in this area to the present day. The presence of white and lodgepole pines with 18 and 8 per cent at the top, indicates their proximity to the bog now. The former is scattered throughout the forest in adjacent montane areas, and the latter exists in pure stands where the forest has been removed by lumbering or fire. An increase of grass from 4 per cent at 0.5 meter to 15 per cent at the top may also be explained by the removal of the forest cover in recent

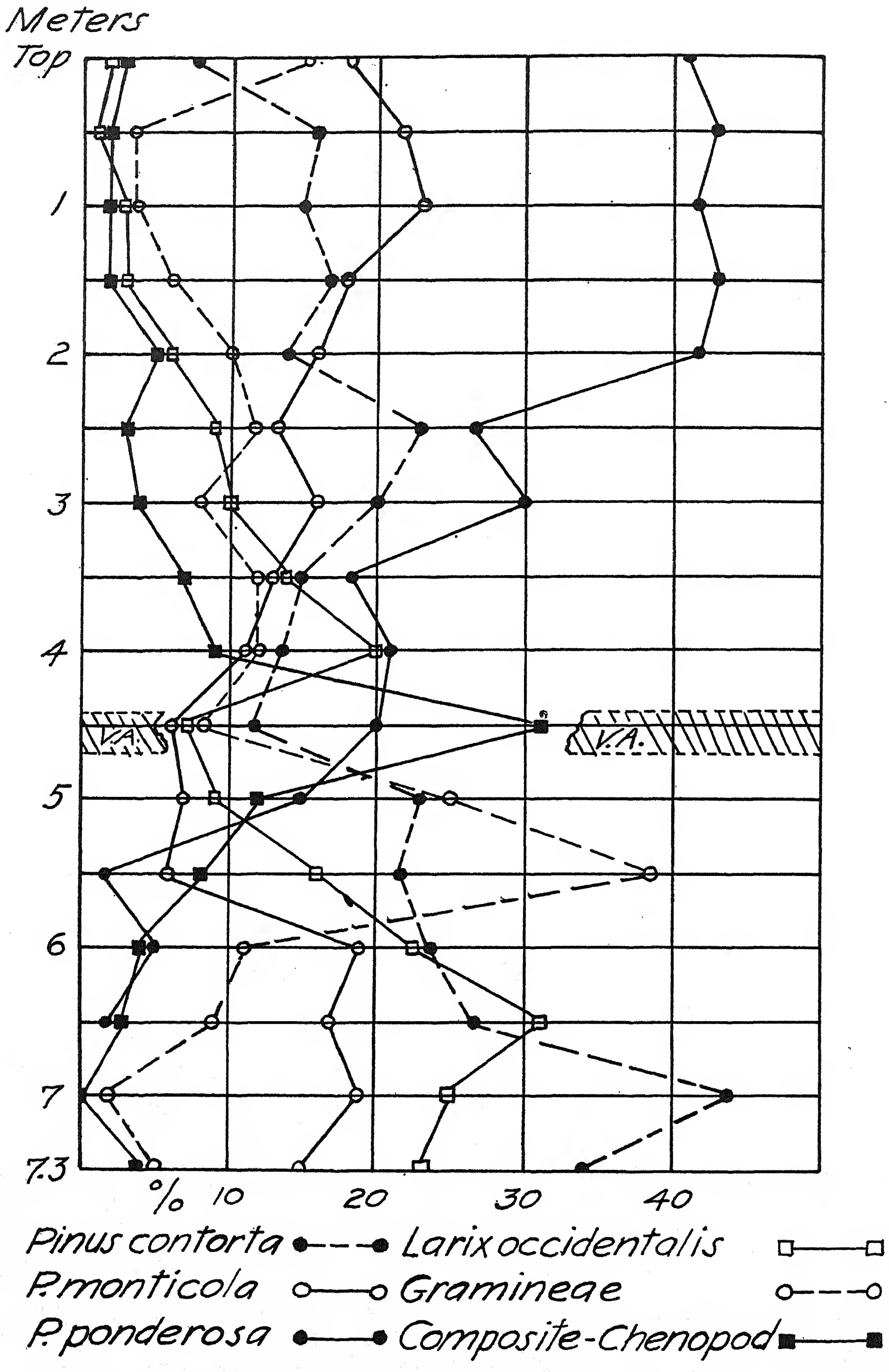

Fig. 1. Pollen diagram.

times by man. The existence of other conifers in the area at present is to be noted by their low percentages in the upper most level (table 1). An abundance of maple (*Acer glabrum*) apparently existed near the bog during its early development, but became less abundant during postglacial time. Alder, willow, and birch were also present to some extent (table 1). Douglas fir and western hemlock played an inconspicuous rôle in postglacial forest succession in this area. The climate was evidently too dry, because these two species were dominant during most of postglacial time in the Puget Sound region (Hansen 1938). The tolerance of evergreens for shade is an important factor, and forest succession in the Northwest may be dependent upon their relative tolerance as much as climate.

TABLE 1

Principal pollens

DEPTH IN METERS	7.3	7.0	6.5	6.0	5.5	5.0	4.5	4.0	3.5	3.0	2.5	2.0	1.5	1.0	0.5	Top
Pinus contorta	34	44	27	24	22	23	12	14	15	20	23	14	17	15	16	8
P. ponderosa			2	5	2	15	20	21	18	30	27	42	43	42	43	41
P. monticola	15	19	17	19	6	7	6	11	13	16	13	16	18	23	22	18
Pseudotsuga mucronata			1	2	1	2	1	2	2	2	4	1	2	2	3	3
Larix occidentalis	23	25	31	23	16	9	7	20	14	10	9	6	3	3	1	2
Abies grandis	2	1						3	3	1	1	1	1	2	4	2
Picea engelmanni	7	2	1			1	1	1	1	2	1		1	1	1	
Tsuga heterophylla				1		1	1	1					1	1	1	1
Gramineae	5	2	9	11	38	25	8	12	12	8	12	10	6	4	4	15
Compositae	2		2	2	4	2	15	5	3	2	3	3	1	2	1	1
Chenopodiaceae	2		1	2	4	10	16	4	4	2		2	1	1	1	2
Alnus	9	5	8	10	2	4	7	5	8	3	6	6	3	3	2	4
Salix	1		1		1	1	4	1	5	1	1		1		1	1
Acer*	56	12	12	16	21	22	60	30	30	18	8	7	9	1	1	1
Betula*	1				2	1		5	2	5	13	2	7	6	1	2
Nymphaea*			3	15	26	1			1	9	9	2		1		1

* Number, not computed in the percentages.

SUMMARY

Pollen analysis of a post-Wisconsin bog in Northeastern Washington in a western yellow pine climax, shows several stages of postglacial forest succession and climate.

A pioneer forest consisting chiefly of lodgepole and western white pines and western larch, with a preponderance of the former, indicates an initial cool and medium dry period.

The first period was followed by one of increasing warmth and dryness, resulting in an extension of the treeless Arid Transition zone, as evidenced by a preponderance of grass pollen at 5.5 meters.

The next period was one of further drying and warming, causing an

extension of the Upper Sonoran zone, as shown by the high percentages of chenopods and composites at 4.5 meters.

The xerothermic period was succeeded by one of increasing coolness and moisture, which brought favorable conditions for the increase of yellow, white, and lodgepole pine forests.

A final period of coolness and medium dryness has existed during the time represented from the 2.0 meter level to the surface or present time. This period was characterized by a climax forest of western yellow pine, with some lodgepole and white pine, and other conifers, and was probably warmer than the initial period.

The author expresses his thanks to Mr. C. M. Chapman, Chief Scientific Aid, and Mr. Virgil Moss, Forester, of the U. S. Bureau of Entomology and Plant Quarantine, Spokane, Washington, for their assistance in obtaining the peat samples.

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Mosses of Interior British Guiana

Edwin B. Bartram

(with two figures)

The mosses in the following schedule were collected by Dr. A. C. Smith in central and southern British Guiana under the auspices of the New York Botanical Garden, the Arnold Arboretum and the Yale School of Forestry, together with the American Museum of Natural History Terry-Holden Expedition.

This previously essentially unexplored country, projecting like a tongue into the State of Para, Brazil, almost to the equator, might naturally be expected to support a moss flora closely resembling that of the Amazonian regions, but instead, a considerable number of the species represented in Dr. Smith's collections are decidedly more suggestive of the Caribbean mosses in a broad sense. This is particularly true of the highlands in the Kanuku and Akarai Mountains with elevations up to 900 meters.

Of the forty-eight species detailed below seventeen, or more than one-third of the total, range north to Florida, and twenty-five, or slightly more than half, are not represented in Mr. Richard's list published in 1934.[1] Ninety-one species including the Sphagna are credited to British Guiana in these two lists, evidently considerably less than the actual moss flora that may be reasonably expected even from such a comparatively limited area.

Where not indicated to the contrary the collections cited are from British Guiana. The types of the new species described are in the writer's herbarium and duplicates are in the herbarium of the New York Botanical Garden. I am indebted to the kindness of Mr. R. S. Williams for the loan of specimens from the New York Botanical Garden for comparative study.

FISSIDENTACEAE

Fissidens radicans Mont. Western extremity of Kanuku Mountains, in drainage of Takutu River, dense forest, alt. 700 m. *3325*.

Distribution: Florida, Mexico, Guatemala, Puerto Rico.

DICRANACEAE

Campylopus savannarum C. M. Northwestern portion of Kanuku Mountains, Mount Iramaikpang, open rocky summit, alt. 975 m., *3645*, abundant on rocks; *3656*, among roots of *Doryopteris*.

Distribution: Costa Rica, Surinam.

[1] Richards, P. W. Musci collected by the Oxford Expedition to British Guiana in 1929. Kew Bull. **1934:** 317–337. 1934.

Holomitrium arboreum Mitt. Northern slope of Akarai Mountains, in drainage of Shodikar Creek, (Essequibo tributary), dense forest, on tree trunk, alt. 300–600 m., *2917*.

Distribution: Mexico to Bolivia, cordilleran.

Leucoloma serrulatum Brid. Northwest portion of Kanuku Mountains, Mount Iramaikpang, dense forest, on tree trunks, alt. 650–850 m., *3600a*, *3614*, *3615a*.

Distribution: Antilles, Mexico to Costa Rica.

Leucoloma tortellum (Mitt.) Jaeg. Western extremity of Kanuku Mountains, in drainage of Takutu River, dense forest, on rocks, alt. 250 m., *3118*. Northwestern portion of Kanuku Mountains, Mount Iramaikpang, dense forest, on rocks along stream, alt. 650 m., *3673*.

As far as I know neither *L. serrulatum* nor *L. tortellum* have been recorded from South America before. The following sporophyte characters are taken from *3673* in which the capsules are all deoperculate and rather old. Perichaetial leaves slightly longer than the stem leaves, abruptly narrowed from a broad, short, clasping base to a slender, linear point, serrulate near the apex and unbordered. Seta erect, smooth, dark red, scarcely 1 cm. long; capsule erect, cylindric, urn about 2 mm. long; peristome teeth reddish, faintly papillose below (capsules overripe, peristome teeth worn and eroded); spores greenish, papillose, 15–20 μ. Probably dioicous, antheridial flowers not seen.

LEUCOBRYACEAE

Octoblepharum albidum Hedw. Basin of Rupununi River, Isherton, lat. about 2°20′N., on bark of *Curatella americana*, savanna, *2510*. Western extremity of Kanuku Mountains, in drainage of Takutu River, alt. 700 m., on charred tree trunks, *3311*. Northwestern slope of Kanuku Mountains, in drainage of Moku-moku Creek (Takutu tributary), dense forest, on palm trunk, alt. 150–400 m., *3566*. Northwestern portion of Kanuku Mountains, Mount Iramaikpang, dense forest, on tree trunks, alt. 650 m., *3676*.

Distribution: Cosmopolitan in tropical regions, north to Florida.

Octoblepharum cylindricum Schp. Basin of Kuyuwini River (Essequibo tributary), about 150 miles from mouth, dense forest, on tree trunks, *2603*.

Distribution: Mexico, Colombia, Brazil.

Leucobryum Martianum (Hornsch.) Hampe. Basin of Essequibo River, near mouth of Onoro Creek, lat. about 1°35′N., dense forest, on fallen log, on high land, *2706a*. Brazil: State of Para: southern slope of Akarai Mountains, in drainage of Rio Mapuera (Trombetas tributary), dense forest, on decayed log, alt. 500–700 m., *2929*, *2951a*.

Distribution: Antilles and Northern South America.

CALYMPERACEAE

Syrrhopodon prolifer Schwaegr. Brazil: State of Para: southern slope of Akarai Mountains, in drainage of Rio Mapuera (Trombetas tributary), dense forest, on decaying wood, alt. 500–700 m., *2951*.

Distribution: Colombia, Brazil.

Syrrhopodon ligulatus (Mont.) Mitt. Western Extremity of Kanuku Mountains, in drainage of Takutu River, dense forest, on charred tree trunks, alt. 700 m., *3311a*.

Distribution: Florida, Guadeloupe.

Syrrhopodon rigidus Hook. & Grev. Basin of Kuyuwini River (Essequibo tributary), about 150 miles from mouth, dense forest, on tree trunks, *2603a*.

Distribution: Antilles to northern Brazil.

Syrrhopodon incompletus Schwaegr. Northwestern slope of Kanuku Mountains, in drainage of Moku-moku Creek (Takutu tributary), dense forest, on palm trunk, alt. 150–400 m., *3565*.

Distribution: Florida to northern South America, Mexico and Central America.

Calymperes Richardi C. M. Basin of Rupununi River, near mouth of Charwair Creek, lat. about 2°35′N., on fallen tree, forest, *2339*.

Distribution: Florida to Brazil, Mexico and Central America.

Calymperes (*Stenocycla*) **Smithii** sp. nov. (fig. 1). Olivaceum, laxe gregarium. Caulis circa 1 cm altus. Folia patentia. 3–3.5 mm. longa, e basi brevi latissime obcuneata, abrupte oblongo-ovata, acuta; marginibus medio folio minute denticulatis, prope apicem serratis; cellulae rotundatae, 8–10 μ, convexae, haud incrassatae, subpellucidae; costa valida, inferne laevis, superne papillosa, prope apicem dorso serrata, cum apice soluta; cancellina breviter obovata, apice rotundata, 10–14-seriata; teniola distincta, flavida, marginata, 4–5-seriata.

Laxly gregarious plants, olivaceous tinged with brown. Stems about 1 cm. high, simple. Leaves curved when dry, spreading when moist, 3–3.5 mm. long and slightly over 0.5 mm. wide at the broadest part of the blade, abruptly oblong-ovate from a short, broad, obcuneate base, broadly acute; margins erect, minutely toothed in the median portion, narrowly winged above and serrate with the teeth in pairs, denticulate and undulate at the leaf shoulders; cells rounded, 8–10 μ, convex on the free surfaces, not incrassate; costa strong, brownish, percurrent, smooth below, papillose above and toothed on the back near the apex. Cancellina forming a short obovate group rounded above and extending scarcely half way up the leaf base, sharply differentiated from the lamina cells; teniola distinct, forming a yellowish border 4 or 5 rows wide at the leaf shoulders and entirely marginal without any shorter cells along the outer edges. Fruit unknown.

Brazil-British Guiana Boundary: Akarai Mountains, height of land between drainage of Rio Mapuera (Trombetas tributary) and Shodikar Creek (Essequibo tributary), dense forest, on tree trunk alt. 600–800 m., *A. C. Smith 2985*, type Jan. 19, 1938.

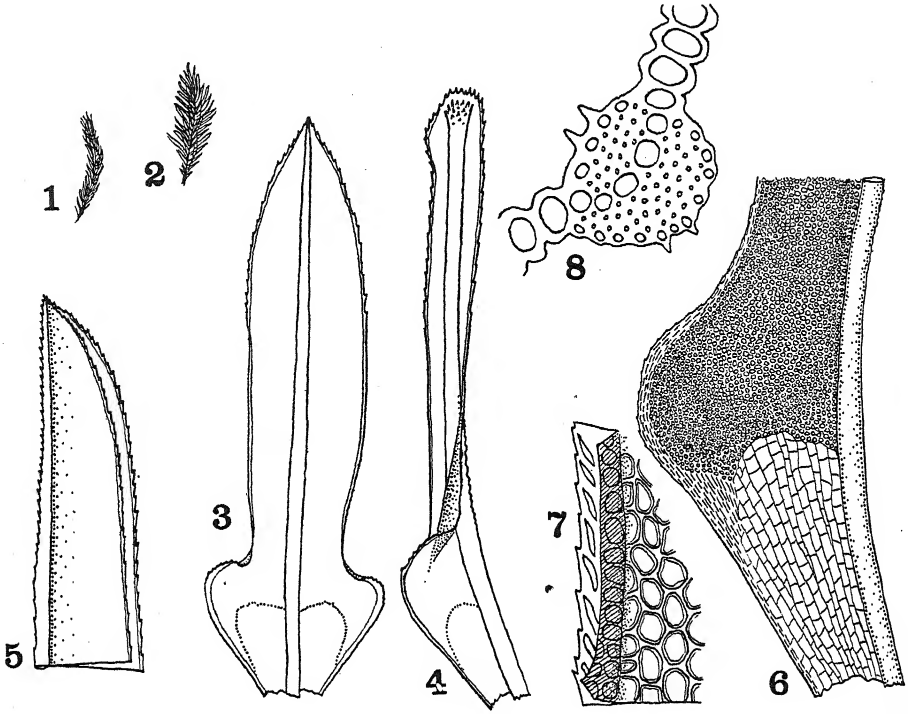

Fig. 1. *Calymperes Smithii* Bartram
1. Dry plant (×1⅓).
2. Moist plant (×1⅓).
3. Leaf (×24).
4. Abnormal leaf (×24).
5. Apex of leaf (×63).
6. One side of leaf base (×63).
7. Leaf cells and margin about one-third down (×330).
8. Cross section of costa, upper half of leaf (×330).

This species differs widely from *C. Sprucei* Besch., as represented by Spruce's Musc. Amaz. et And. 20, in the short, obcuneate leaf base with the cancellina group extending only about half way up to the leaf shoulders, the marginal teniolae and the strongly serrate apical margins of the blade.

Calymperes Donnellii Aust. Western extremity of Kanuku Mountains, in drainage of Takutu River, dense forest, on tree trunks, alt. 700 m., *3325a*, *3198*, on rocks.

Distribution: Florida, Antilles, northern South America, Central America, Cocos Island.

Calymperes nicaraguense Ren. & Card. Basin of Essequibo River, lat. about 6°7′N., Head Falls, on humus, edge of forest, *2105*.

Distribution: British Honduras, Nicaragua, Guatemala, Costa Rica.

Calymperes disciforme C. M. Northwestern portion of Kanuku Mountains, Mount Iramaikpang, dense forest, on tree trunks, alt. 650 m., *3676a*, mixed with *Octoblepharum albidum*.

Distribution: Santo Domingo, Panama, Colombia.

Calymperes lonchophyllum Schwaegr. Basin of Essequibo River, near mouth of Onoro Creek, lat. about 1°35′N., dense forest, on tree trunks along river, *2688*. Brazil-British Guiana Boundary: Akarai Mountains, height of land between drainage of Rio Mapuera (Trombetas tributary) and Shodikar Creek (Essequibo tributary), dense forest on tree trunk, alt. 600–800 m., *2994*.

Distribution: Antilles, British Honduras, Guatemala, Costa Rica, Venezuela, Brazil.

POTTIACEAE

Hyophila tortula (Schwaegr.) Hampe. Western extremity of Kanuku Mountains, in drainage of Takutu River, dense forest, on exposed rock ledges, alt. 300 m., *3132*.

Distribution: wide in tropical America, eastern and southern United States, central Europe.

Bryum coronatum Schwaegr. Basin of Rupununi River, near mouth of Charwair Creek, lat. about 2°35′N., on fallen tree, forest, *2338*. Basin of Rupununi River, Wichabai, lat. about 2°52′N., on humus, patch of forest in savanna, *2295*.

Distribution: Cosmopolitan in tropical regions extending north to Florida.

Rhodobryum Beyrichianum (Hornsch.) Par. Western extremity of Kanuku Mountains, in drainage of Takutu River, dense forest, on decaying log, alt. 600 m., *3282*.

Distribution: tropical and subtropical South America, north to Central America and Mexico.

ORTHOTRICHACEAE

Macromitrium mucronifolium (Hook. & Grev.) Schwaegr. Western extremity of Kanuku Mountains, in drainage of Takutu River, dense forest, on tree trunk, alt. 400 m., *3148*. Northwestern slopes of Kanuku Mountains, in drainage of Moku-moku Creek (Takutu tributary), dense forest, on tree trunks, alt. 150–400 m., *3481*, *3544a*.

Distribution: Florida, Antilles, Mexico to Ecuador, Galapagos Islands.

Macromitrium stellatum (Hook. & Grev.) Brid. Basin of Rupununi River, near mouth of Charwair Creek, lat. about 2°35′N., on tree trunks, forest, *2339a*, *2382*. Northwestern slopes of Kanuku Mountains, in drainage of Moku-moku Creek (Takutu tributary), dense forest, on tree trunk, *3544*.

Distribution: Brazil, Bolivia. If *Macromitrium tumidulum* Mitt. proves to be synonymous with this species, as seems very probable, the range would include Peru, Jamaica and Haiti.

LEUCODONTACEAE

Pseudocryphaea flagellifera (Brid.) E. G. Britt. Northwestern slopes of Kanuku Mountains, in drainage of Moku-moku Creek (Takutu tributary), dense forest, on twigs, alt. 150–400 m., *3546*.

Distribution: Florida, Antilles, Brazil, Mexico, Guatemala, Costa Rica.

PTEROBRYACEAE

Orthostichopsis crinita (Sull.) Broth. Northwestern portion of Kanuku Mountains, Mount Iramaikpang, dense forest, on twigs, alt. 700 m., *3604*.

Distribution: Cuba, Venezuela, Peru, Ecuador, Bolivia.

Orthostichopsis tetragona (Sw.) Broth. Northern slope of Akarai Mountains, in drainage of Shodikar Creek (Essequibo tributary), dense forest, on tree trunk, alt. *300–600* m., *2918*.

Distribution: Antilles, northern South America, Mexico, Central America.

Pireella cymbifolia (Sull.) Card. Western extremity of Kanuku Mountains, in drainage of Takutu River, dense forest, on tree trunk, alt. 200 m., *3248a*.

Distribution: Florida, Alabama, Louisiana, Antilles, Mexico to Costa Rica. Just a few plants growing with *Neckeropsis undulata*, but enough to establish a new record for South America, as far as I know.

METEORIACEAE

Meteoriopsis patula (Hedw.) Broth. Northwestern slopes of Kanuku Mountains, in drainage of Moku-moku Creek (Takutu tributary), dense forest, on twigs, alt. 150–400 m., with *Pseudocryphaea flagellifera*, *3546a*.

Distribution: wide in tropical America, north to Florida.

NECKERACEAE

Neckeropsis undulata (Hedw.) Reichdt. Western extremity of Kanuku

Mountains, in drainage of Takutu River, dense forest, on tree trunk, *3248*.

Distribution: wide in tropical America, north to Florida.

PILOTRICHACEAE

Pilotrichum bipinnatum (Schwaegr.) Brid. Basin of Essequibo River, near mouth of Onoro Creek, lat. about 1°35′N., on twigs, in swamp, *2795*.

Distribution: Antilles, Brazil, Venezuela, Nicaragua to Peru.

HOOKERIACEAE

Callicostella rufescens Mitt. Basin of Shodikar Creek (Essequibo tributary), lat. about 1°18′N., dense forest, on tree trunks, on low land, *2856*.

Distribution: Trinidad, Surinam, Brazil, Ecuador.

Callicostella depressa (Hedw.) Jaeg. Western extremity of Kanuku Mountains, in drainage of Takutu River, dense forest, on decayed log, alt. 600 m., *3194*.

Distribution: Antilles.

Hookeropsis Parkeriana (Hook.) Jaeg. Basin of Essequibo River, near mouth of Onoro Creek, lat. about 1°35′N., on twigs, in swamp, *2793*.

Distribution: Barbados to eastern Brazil.

PLAGIOTHECIACEAE

Stereophyllum leucostegium (Brid.) Mitt. Basin of Rupununi River, near mouth of Charwair Creek, lat. about 2°35′N., on rocks, edge of forest, *2369*.

Distribution: wide, Antilles to Brazil, Mexico to northern South America.

Stereophyllum radiculosum (Hook.) Mitt. Western extremity of Kanuku Mountains, in drainage of Takutu River, dense forest, on boulders, alt. 700 m., *3326*.

Distribution: Mexico to Peru, Venezuela, Brazil.

Pilosium flaccisetum C.M. Basin of Essequibo River, near Mouth of Onoro Creek, lat. about 1°35′N., on decayed wood in swamp, *2748*.

Distribution: Endemic?

SEMATOPHYLLACEAE

Rhaphidorrhynchium subsimplex (Hedw.) Broth. Basin of Kuyuwini River (Essequibo tributary), about 150 miles from mouth, dense forest, on tree trunks and decaying wood, *2520*, *2525*, *2604*. Western extremity of Kanuku Mountains, in drainage of Takutu River, dense forest, alt. 150–200 m., on tree trunks, *3088*, *3357*. Northwestern slopes of Kanuku

Mountains, in drainage of Moku-moku Creek (Takutu tributary), dense forest, on tree trunks, alt. 150–400 m., *3415*. Northwestern portion of Kanuku Mountains, Mount Iramaikpang, dense forest, on decaying bark, alt. 900 m., *3630*. Brazil-British Guiana Boundary: Akarai Mountains, height of land between drainage of Rio Mapuera (Trombetas tributary) and Shodikar Creek (Essequibo tributary), dense forest, on decaying wood, alt. 600–800 m., *2976*.

Distribution: wide in tropical America.

Sematophyllum loxense (Hook.) Mitt. Northwestern portion of Kanuku Mountains, Mount Iramaikpang, dense forest, on humus, alt. 650 m., *3672a*.

Distribution: wide in tropical America.

Sematophyllum caespitosum (Hedw.) Mitt. Western extremity of Kanuku Mountains, in drainage of Takutu River, dense forest, on rocks, alt. 200 m., *3220*.

Distribution: wide in tropical America, north to Florida.

Rhaphidostichum (*Rhaphidostichella*) **guianense** sp. nov. (fig. 2). Autoicum; caespitosum, caespitibus depressis, sat densis, fuscescenti-viridibus, nitidus. Caulis elongatus, inferne denudatus, irregulariter ramosus, ramis vix 1 cm. longis, cuspidatis. Folia patentia, ecostata, oblongo-ovata, 2–2.3 mm. longa et 0.65 mm. lata, sensim in acumen subintegerrimum contracta; marginibus erectis, superne late inflexis, integerrimis vel prope apicem minutissime denticulatis; cellulae lineares, laevissimae, haud incrassatae, alares 3 vel 4, magnae, oblongae, aurantiacae. Perichaetii brachteae erectae, ad 2 mm. longae, internae longe acuminatae, superne denticulatae; seta circa 2 cm. longa, superne humiliter pustulosa; theca horizontalis, minuta, deoperculata 1 mm. longa.

Autoicous; brownish green, glossy plants, paler at the tips, growing in rather dense tufts or mats. Stems elongate, creeping, denuded of leaves below, irregularly branched, the branches scarcely 1 cm. long, densely foliate, cuspidate at the tips, about 3 mm. wide with leaves. Leaves crowded, spreading, ecostate, oblong-ovate, concave, 2–2.3 mm. long and 0.65 mm. wide, gradually contracted to a rather short, nearly entire, sharply pointed acumen; margins erect, often broadly inflexed above, entire or minutely denticulate in the upper third; cells linear, smooth, not incrassate, alar group of 3 or 4 large oblong cells, usually deeply colored. Perichaetium erect, about 2 mm. high, the inner leaves gradually contracted to a long denticulate acumen. Seta about 2 cm. high, very indistinctly pustulose toward the apex; capsule horizontal, ovoid with a short neck, the urn 1 mm. long; peristome teeth with a fine zigzag median line.

Western extremity of Kanuku Mountains, in drainage of Takutu River, dense forest, alt. 250 m., on rocks, *3119*. Northwestern portion of Kanuku Mountains, Mount Iramaikpang, dense forest, on rocks, alt. 900 m., *3632a*, *3635*, type (Apr. 22, 1938), on decayed wood.

Although evidently allied in leaf structure to *R. Schwaneckianum* C.M. of Cuba and Puerto Rico, this species is quite distinct in the autoicous inflorescence and the shorter, less ligulate and nearly entire leaf acumen.

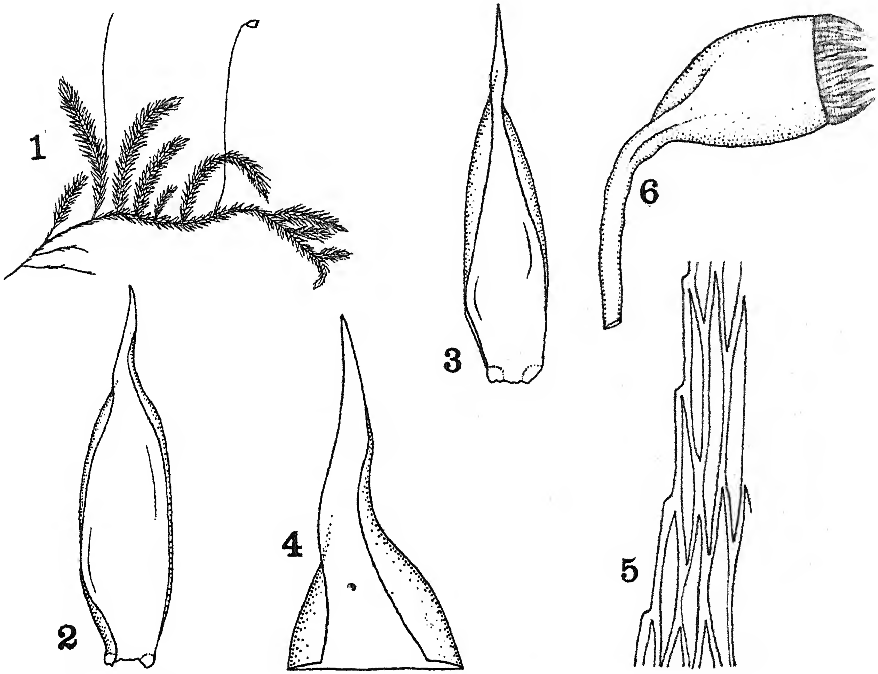

Fig. 2. *Rhaphidostichum guianense* Bartram
1. Plant (×1⅓).
2, 3. Leaves (×22).
4. Apex of leaf (×63).
5. Upper leaf cells and margin (×330).
6. Moist capsule (×20).

Acroporium guianense (Mitt.) Broth. Brazil: State of Para: southern slope of Akarai Mountains, in drainage of Rio Mapuera (Trombetas tributary), dense forest, on bark of tree, alt. 500–700 m., *2949a*.

Distribution: Guiana, Brazil.

Acroporium pungens (Hedw.) Broth. Basin of Kuyuwini River (Essequibo tributary), about 150 miles from mouth, dense forest, on fallen log, *2636*. Basin of Essequibo River, near mouth of Onoro Creek, lat. about 1°35′N., dense forest, on twigs, on high land, *2760*.

Distribution: wide in Antilles and tropical America.

Potamium vulpinum (Mont.) Mitt. Basin of Kuyuwini River (Essequibo tributary), about 150 miles from mouth, dense forest, on dead branches along river, *2565*.

Distribution: French Guiana, Brazil.

Taxithelium planum (Brid.) Mitt. Basin of Essequibo River, lat. about 6°7′N., Head Falls, on humus, edge of forest, *2107*, a closely pinnate, plumose form. Basin of Rupununi River, near mouth of Charwair Creek, lat. about 2°35′N., on tree trunks, wet forest, *2383*. Basin of Rapununi River, Isherton, lat. about 2°20′N., on decaying wood, dense forest, *2498*. Basin of Kuyuwini River (Essequibo tributary), about 150 miles from mouth, dense forest, on decaying wood, *2546*, *2574*. Basin of Essequibo River, near mouth of Onoro Creek, lat. about 1°35′N., dense forest on tree trunks along river, *2649*, *2655*, on rocks and sand along river, *2644*, on decayed log along river. Basin of Shodikar Creek (Essequibo tributary), lat. about 1°18′N., on decaying log, *2878*. Northern slope of Akarai Mountains, in drainage of Shodikar Creek (Essequibo tributary), dense forest, on tree roots, *2895*.

Distribution: wide in tropical America, north to Florida.

Trichosteleum ambiguum (Schwaegr.) Broth. Northwestern portion of Kanuku Mountains, Mount Iramaikpang, dense forest, on tree trunks, alt. 900 m., *3629*. Brazil-British Guiana Boundary: Akarai Mountains, height of land between Rio Mapuera (Trombetas tributary) and Shodikar Creek (Essequibo tributary), dense forest, on bark of tree, alt. 600–800 m., *2975a*.

Distribution: Brazil, Peru.

HYPNACEAE

Rhacopilopsis trinitensis (C.M.) E. G. Britt. & Dix. Northwestern portion of Kanuku Mountains, Mount Iramaikpang, dense forest, on tree trunk, alt. 850 m., *3618*.

Distribution: Costa Rica, Panama, Trinidad, French Guiana, tropical Africa, Madagascar.

Vesicularia amphibola (Spr.) Broth. Basin of Shodikar Creek (Essequibo tributary), lat. about 1°18′N., dense forest, on sand-covered log, low land, *2854*.

Distribution: Florida, Antilles, Brazil.

Mittenothamnium diminutivum (Hampe) E. G. Britt. Basin of Rupununi River, Isherton, lat. about 2°20′N., on tree trunk, dense forest. *2497*. Western extremity of Kanuku Mountains, in drainage of Takutu River, dense forest, on log and tree trunk, alt. 200–600 m., *3093*, *3197*.

Distribution: wide in tropical America, north to Florida.

BUSHKILL, PA.

Studies of South American Plants—VI. Preliminary notes on Hippocrateaceae

A. C. Smith

The tropical American species of Hippocrateaceae have been much neglected, having been studied in detail only by Miers[1] and Peyritsch,[2] neither of whose works is adequate for a present understanding of the American species. Considerable disagreement as to generic limits is apparent, not only in these two works, but in earlier considerations of the family. The 17 genera recognized by Miers were distributed between *Hippocratea* and *Salacia* by Peyritsch. The present writer is inclined to agree with Peyritsch's treatment, at least for the present, although it must be admitted that many of Mier's genera have clear-cut floral characters which, if magnified many times, might be thought generic by most botanists. This attitude must be modified, however, by the inclusion of several species which appear to break down parts of Miers' classification. The writer plans to undertake monographic work on the family in the near future and will appreciate the long-term loan of American material.

Recent collections in Amazonian Brazil by Mr. B. A. Krukoff have disclosed no fewer than 17 undescribed species of *Salacia*. The fact that these collections have nearly doubled the number of known Amazonian species of the genus will readily be understood by those familiar with tropical collecting. The species of *Salacia* are for the most part high-climbing lianas with very small inconspicuous flowers; such plants are obtainable only by chance unless the collector is making a systematic exploration of high forest trees and lianas, with a large crew at his disposal. During his trip to the Solimoes region in 1936 Mr. Krukoff was paying close attention to the Hippocrateaceae, at the writer's request, and this work was facilitated by his search for species of *Strychnos* and Menispermaceae, plants of similar habit.

The present paper is planned to propose these 17 species, all of which were collected in Brazil; all types are deposited in the herbarium of the New York Botanical Garden, and duplicates are widely distributed. The remaining Amazonian species, including a few from Peru and Venezuela which may be expected in adjacent Brazil, are listed. In the discussions which follow, all mention of Miers and Peyritsch refers to their works above listed. In the key, the generic names in parentheses refer to Miers'

[1] Miers, J. On the Hippocrateaceae of South America. Trans. Linn. Soc. **28:** 319–432. *pl. 16–32*. 1872.

[2] Peyritsch, J. Hippocrateaceae. Mart. Fl. Bras. **11**(1): 125–164. *pl. 42–49*. 1878.

treatment. Mention of fruit characters is omitted from the key, since fruit of only a few species is known.

KEY TO THE AMAZONIAN SPECIES OF SALACIA

Stigmas opposite the stamens.
  Disk discontinuous, forming staminiferous pockets.
    Stamens, stigmas, and locules 3 (*Kippistia*).
      Stigmas narrow, often linear, not lobed.
        Inflorescence paniculate, the primary rachis straight and obvious; usually shrubs or small trees.
          Young branchlets terete; venation of leaf blades often obscure; petals opaque.... ....1. *S. cognata.*
          Young branchlets angled; venation of leaf blades conspicuous; petals lineolate.... ....2. *S. lineolata.*
        Inflorescence dichotomously branching; lianas.
          Internodes of inflorescence freely articulate, very short; leaf margins serrate....... ....3. *S. articulata.*
          Internodes of inflorescence not articulate; leaf margins entire or obsoletely crenate.
            Peduncles solitary in leaf axils, several times dichotomously branched.
              Leaf blades with obscure veinlets; inflorescence broadly spreading and more or less hemispherical, 9- or 10-times dichotomously branched......4. *S. diffusiflora.*
              Leaf blades with prominulous veinlets; inflorescence stiff, not conspicuously spreading, 5–7-times dichotomously branched..........5. *S. minutiflora.*
            Peduncles several from base of inflorescence, once or twice dichotomously branched. ....6. *S. pedunculata.*
      Stigmas broad, bilobed.
        Leaf blades elliptic-oblong; inflorescence 1.5–2.5 cm. long, not conspicuously divaricate; petals glabrous...7. *S. Krukovii.*
        Leaf blades broadly elliptic; inflorescence 6–8 cm. long, divaricately branched; petals minutely pilose without.....................................8. *S. divaricata.*
    Stamens, stigmas, and locules 5 (*Cheiloclinium*)........................9. *S. anomala.*
  Disk continuous, short tubular (*Amphizoma*).
    Stigmas bilobed.
      Petioles 4–8 mm. long; inflorescence slender, lax, the flowers long (6–8 mm.) pedicellate. ....10. *S. laxiflora.*
      Petioles 10–15 mm. long; inflorescence stiff, the flowers short (1–3 mm.) pedicellate.... ....11. *S. Martiana.*
    Stigmas entire..12. *S. congestiflora.*
Stigmas alternate with the stamens or obscure.
  Disk short tubular, thin carnose or submembranous.
    Anther locules contiguous, dehiscing by confluent horizontal clefts, the connective obscure (*Tontelea*).
      Stigmas obvious, entire.
        Leaf blades ovate- or elliptic-oblong, 8–17 by 2.5–7 cm.; flowers 3–4 mm. in diameter; petals entire or erosulous..................................13. *S. attenuata.*
        Leaf blades lanceolate- or elliptic-oblong, 8–9 by 2.5–3.5 cm.; flowers about 3 mm. in diameter...14. *S. corymbosa.*
        Leaf blades broadly elliptic-oblong, 16–25 by 6–12 cm.; flowers about 2 mm. in diameter; petals erose-fimbriate.....................................15. *S. mauritioides.*
      Stigmas obscure.
        Inflorescence lax, long (to 9 cm.) pedunculate; flowers 6–7 mm. in diameter; leaves chartaceous, conspicuously veined.........................16. *S. cylindrocarpa.*

Inflorescence short (to 2 cm.) pedunculate; flowers not more than 4 mm. in diameter.
Petioles 10–13 mm. long; leaf blades obtuse at base, smooth; sepals pilose within. . . . .17. *S. nectandrifolia.*
Petioles 13–25 mm. long; leaf blades attenuate or acute at base, rugulose; sepals glabrous..18. *S. petiolata.*
Anther locules distinct, dehiscing by longitudinal clefts, exceeded by the connective (*Peritassa*).
Disk single.
Inflorescence branches pubescent.................................19. *S. Colasi.*
Inflorescence branches glabrous.
Leaf blades attenuate at base, crenate-serrate at margin............20. *S. dulcis.*
Leaf blades rounded to acute at base, entire to undulate-crenate at margin......... ....21. *S. laevigata.*
....22. *S. amazonica.*
Disk double, forming two concentric rings...........................23. *S. Ulei.*
Disk pulvinate, carnose; flowers often fasciculate.
Disk highly conical-pulvinate (*Thermophila*).
Inflorescence freely branching; disk free at summit.
Leaves chartaceous, not larger than 17 by 10 cm.; flowers 8–11 mm. in diameter; petals plane; disk truncate at apex.................................24. *S. obovata.*
Leaves thick coriaceous, up to 50 by 20 cm.; flowers less than 3 mm. in diameter; petals distally thickened and tuberculate; disk dentate at apex.........25. *S. acreana.*
Flowers fasciculate; disk adnate to ovary by interstaminal septae......26. *S. caloneura.*
Disk annular-pulvinate, broadly expanded at base (*Raddia*).
Flowers fasciculate.
Flowers 26–30 mm. in diameter at anthesis; leaf blades attenuate at base............ ....27. *S. macrantha.*
Flowers less than 21 mm. in diameter at anthesis.
Disk 3–5 mm. in diameter; flowers more than 10 mm. in diameter at anthesis.
Flowers on stem: leaf blades narrowly oblong, 3–4.5 cm. broad, subacute or obtuse at base...28. *S. cauliflora.*
Flowers axillary; leaf blades rarely less than 5 cm. broad.
Leaf blades rounded and truncate at base, the secondary nerves essentially plane, not conspicuous.
Petals lineolate; leaf blades more than three times as long as broad....... .... 29. *S. polyanthomaniaca.*
Petals opaque; leaf blades about twice as long as broad...30. *S. impressifolia.*
Leaf blades obtuse or somewhat rounded at base, the secondary nerves conspicuous.
Pedicels 12–15 mm. long; flowers about 13 mm. in diameter; style short, attenuate; locules about 6-ovulate......................31. *S. juruana.*
Pedicels 3–3.5 mm. long; flowers 15–18 mm. in diameter; style none; locules 2-ovulate.......................................32. *S. gigantea.*
Disk about 2 mm. in diameter; flowers 5–6 mm. in diameter at anthesis............ ....33. *S. solimoesensis.*
Flowers in a freely branching inflorescence.
Disk elevated at inner margin; style subulate; petiole 6–10 mm. long...34. *S. cuspidata.*
Disk flat; style minute; petiole 3–5 mm. long.......................35. *S. gracilis.*

1. Salacia cognata (Miers) Peyr. in Mart. Fl. Bras. **11** (1): 144. 1878. *Elaeodendron macrophyllum* Rusby, Descr. N. Sp. S. Am. Pl. 24. 1920. *Salacia sphaerocarpa* Rusby, Descr. N. Sp. S. Am. Pl. 52. 1920.

Recent collections extend the range of this species, which both Miers and Peyritsch indicated as limited to southeastern Brazil, to Colombia and Tobago. The specimens cited are remarkably uniform and cannot be distinguished from south Brazilian material. The following specimens, from the northern part of the range of the species, are in the herbarium of the New York Botanical Garden:

TOBAGO: *Broadway 4699; Sandwith 1910.* COLOMBIA: Sur de Santander: Magdalena Valley, *Haught 1385.* VENEZUELA: lower Orinoco, *Rusby & Squires 247, 416* (cotypes of *S. sphaerocarpa*). BRITISH GUIANA: *Smith 2486, 3186, 3603.* BRAZIL: Amazonas: basin of Rio Jurua, *Krukoff 4653, 4843;* basin of Rio Madeira, *Rusby 1248* (type of *Elaeodendron macrophyllum*); *Krukoff 6140, 6188, 6393, 6682.* Maranhão: *Froes 1712.*

2. **Salacia lineolata** sp. nov. Frutex vel arbor gracilis ad 10 m. alta ubique glabra, ramis ut videtur interdum scandentibus; ramulis gracilibus juventute quadrangularibus vel leviter 4-alatis viridibus mox teretibus fuscis lenticellis verruculosis, ad axillas paullo dilatatis; foliis oppositis, petiolis crassis rugosis supra canaliculatis 3–7 mm. longis, laminis chartaceis viridibus (subtus pallidioribus) oblongis vel anguste elliptico-oblongis, 14–23 cm. longis, 4–8 cm. latis, basi obtusis petiolo decurrentibus, apice caudato-acuminatis (acumine 15–25 mm. longo augusto obtuso), margine leviter revolutis integris vel apicem versus obscure crenatis, costa utrinque prominente, nervis lateralibus utroque 8–12 arcuato-adscendentibus prope margines obscure anastomosantibus supra conspicue prominulis subtus prominentibus, venulis manifeste subtile reticulatis utrinque prominulis; paniculis axillaribus 1.5–3 cm. longis pauciramosis, bracteis coriaceis elongato-deltoideis acutis 1.7–2 mm. longis; pedicellis rectis circiter 2 mm. longis, bracteolis 2 deltoideis acutis circiter 1 mm. longis margine erosis; sepalis late deltoideo-ovatis, 0.7–1.5 mm. longis, 1.5–2 mm. latis, interdum minute glanduloso-lineolatis, apice rotundatis, margine minute fimbriatis vel erosis; petalis erectis carnosis obovato- vel spathulato-oblongis, 2.3–2.8 mm. longis, 1.4–2.2 mm. latis, extra irregulariter fusco-lineolatis, intra minute scabridulis, apice rotundatis, margine integris; disco inconspicuo carnoso ad 0.3 mm. alto in labia 3 sacciformia staminigera interruptim laxato; staminibus 3, filamentis ligulatis circiter 0.6 mm. longis, antheris transversaliter ellipsoideis circiter 0.2 mm. longis et 0.3 mm. latis; ovario trigone subgloboso sub anthesi circiter 1.4 mm. diametro; stigmatibus 3 summo ovarii radiatim adnatis, circiter 0.4 mm. longis, apice liberis, staminibus oppositis; drupis oblongo-ellipsoideis ad 33 mm. longis et 19 mm. latis (sed haud dubie maturitate majoribus), saepe leviter falcatis, siccitate glaucis vel fuscis, pericarpio coriaceo 0.6–1 mm. crasso valde ruguloso-punctato, seminibus paucis (circiter 5) superpositis ovatis angulatis, 13–15 mm. longis (maturitate majoribus?), in pulpa nidulantibus.

Type, *Krukoff 8853*, collected in Oct.–Dec., 1936, in basin of Creek Belem, Municipality São Paulo de Olivença, basin of Rio Solimoes,

Amazonas. Other collections are: from the type locality, *Krukoff 9009;* from the same general region, near Palmares, *Krukoff 8318;* Territory Acre: basin of Rio Purus, near mouth of Rio Macauhan (tributary of Rio Yaco), *Krukoff 5732*. Description of the fruit is from the last specimen, collected in September, 1933. All are from high forest on terra firma.

S. lineolata belongs to Section I of Peyritsch (the genus *Kippistia* of Miers), being closely related only to *S. cognata* (Miers) Peyr., from which it is readily distinguished by its angled young branchlets, its more conspicuous leaf venation, and its somewhat larger flowers with the petals and often the sepals conspicuously lineolate rather than smooth and opaque. Probably this species is the same as Peyritsch's variety *egensis* of *S. cognata*, based on *Poeppig 2796*, which I have not seen. Its specific rank seems well merited.

3. **Salacia articulata** sp. nov. Frutex scandens ubique glaber; ramulis oppositis divaricatis juventute purpurascentibus leviter angulatis mox teretibus fuscis; foliis oppositis, petiolis plerumque stramineis rugosis supra profunde canaliculatis 7–10 mm. longis, laminis coriaceis siccitate fusco-viridibus elliptico-oblongis, 8–12 cm. longis, 3–5 cm. latis, basi obtusis vel acutis, apice breviter acuminatis (acumine abrupto 5–10 mm. longo subacuto), margine cartilagineo-incrassatis conspicue serratis (serrationibus 5 vel 6 per centimetrum), supra planis nitidis, subtus parce nigro-punctatis, costa utrinque prominente, nervis lateralibus utroque 8–11 arcuato-adscendentibus supra minute prominulis vel leviter insculptis subtus prominulis, venulis immersis; inflorescentiis axillaribus ad 2 cm. longis breviter (ad 6 mm.) pedunculatis repetitim dichotome multiramosis, ramulis minutissime luteo-punctatis, internodiis articulatis 1–2.2 mm. longis et circiter 1 mm. diametro, bracteis coriaceis late ovatis 0.2–0.4 mm. longis; floribus numerosissimis sessilibus, apicem versus in dichotomiis vel summo pedunculorum ultimorum 2–5 congestis, sub anthesi (petalis erectis vel incurvatis) circiter 1.2 mm. diametro; sepalis late deltoideis, 0.5–0.6 mm. longis, 0.7–0.9 mm. latis, apice acutis, margine erosulis; petalis tenuiter carnosis elliptico-oblongis, 1–1.2 mm. longis, 0.7–0.9 mm. latis, apice obtusis vel rotundatis, margine erosulis, basi ad 0.4 mm. angustatis; disco carnoso in labia 3 sacciformia staminigera 0.15–0.2 mm. alta et circiter 0.3 mm. lata interruptim laxato; staminibus 3, filamentis patulis carnosis ligulatis circiter 0.3 mm. longis, antheris reniformibus circiter 0.12 mm. longis et 0.2 mm. latis, per rimas horizontales terminales dehiscentibus; ovario depresso-subgloboso sub anthesi 0.5–0.6 mm. diametro; loculis 3 ut videtur 4-ovulatis; stigmatibus 3 summo ovarii radiatim adnatis, apice liberis, staminibus oppositis.

Type, *Krukoff 8836*, collected Oct.–Dec., 1936, in high forest on terra firma, basin of Creek Belem, Municipality São Paulo de Olivença, basin of Rio Solimoes, Amazonas. It is a species of Peyritsch's Section I (*Kippistia* Miers), characterized by minute flowers, finely serrate leaves, and

short and conspicuously articulate sections of its inflorescence branches. Its closest relative is *S. diffusiflora* (Miers) Peyr., a species with less conspicuously toothed leaf margins and larger inflorescences with more numerous flowers and with longer slenderer internodes which are not conspicuously articulate. The distal sections of the inflorescence of the new species are so freely articulate as to become readily detached; thus the inflorescence of dried specimens disintegrates into small clusters of several internodes each.

4. SALACIA DIFFUSIFLORA (Miers) Peyr. in Mart. Fl. Bras. **11** (1): 143. *pl. 45*. 1878. Rio Cassiquiare region of Venezuela.

5. **Salacia minutiflora** sp. nov. Frutex scandens ubique glaber; ramulis fuscis subteretibus juventute complanatis; foliis oppositis, petiolis gracilibus rugosis supra canaliculatis 11–17 mm. longis, laminis chartaceis vel tenuiter coriaceis siccitate viridibus oblongo-ellipticis, 12–16 cm. longis, 4.5–7.5 cm. latis, basi acutis vel obtusis, apice breviter cuspidatis (acumine lato ad 7 mm. longo obtuso), margine leviter revolutis integris vel obsolete crenatis, costa utrinque prominente, nervis lateralibus utroque 8–12 arcuato-adscendentibus utrinque valde prominulis, venulis juventute manifeste reticulatis utrinque prominulis maturitate supra obscuris; inflorescentiis axillaribus solitariis 2–3.5 cm. longis repetitim dichotomo-ramosis; pedunculis crassis 2–4 mm. longis, ramulis superne incrassatis ad nodos crassis, bracteis et bracteolis late ovatis subacutis 0.4–1 mm. longis; floribus in dichotomiis pedicellatis (pedicellis gracilibus 2.5–3 mm. longis) vel summo pedunculorum ultimorum 2 vel 3 sessilibus aggregatis (versimiliter sub anthesi omnino pedicellatis); sepalis deltoideis, 0.7–1 mm. longis et latis, apice rotundatis, minutissime vel obscure luteo-punctatis vel breviter lineolatis; petalis (immaturis) oblongis, 0.7–0.9 mm. longis, circiter 0.8 mm. latis, apice obtusis; disco inconspicuo in labia 3 sacciformia staminigera circiter 0.1 mm. alta et 0.25 mm. lata interruptim laxato; staminibus 3, filamentis minutis, antheris transversaliter ellipsoideis circiter 0.25 mm. latis, per rimas horizontales subapicales dehiscentibus; ovario breviter cylindrico vel trigono summo complanato; loculis 3 stigmatibus alternatis ut videtur 2-ovulatis; stigmatibus 3 summo ovarii radiatim adnatis staminibus oppositis.

Type, *Krukoff 8217*, collected Sept.–Oct., 1936, on terra firma near Palmares, Municipality São Paulo de Olivença, basin of Rio Solimoes, Amazonas. Belonging to Section I of Peyritsch (*Kippistia* Miers), the new species is closely related to *S. podostemma* Sandwith, differing by its more compact inflorescence with stouter branches and a very short common peduncle (2–4 mm. rather than 30–50 mm. long). The petals of the new species (although immature) probably even at anthesis are smaller than those of the Guiana species.

6. **Salacia pedunculata** sp. nov. Frutex (demum scandens?) ubique glaber; ramulis fuscis vel cinereis subteretibus ad axillis paullo dilatatis; foliis oppositis, petiolis nigrescentibus striatis supra canaliculatis 10–20 mm. longis, laminis chartaceis vel tenuiter coriaceis siccitate supra viridibus subtus fuscis elongato-ellipticis, 15–25 cm. longis, 4.3–8 cm. latis, basi attenuatis petiolo decurrentibus, apice acuminatis (acumine 1–2 cm. longo obtuso), margine integris leviter revolutis, costa utrinque prominente, nervis lateralibus utroque 8–10 arcuato-adscendentibus prope margines anastomosantibus utrinque valde prominulis, venulis manifeste reticulatis utrinque prominulis; inflorescentiis axillaribus vel e ramulis infra folia orientibus 2–5 cm. longis; pedunculis gracilibus 4–8 e basi distinctis paucifloris semel vel bis dichotome divisis, ad nodos bibracteolatis, bracteolis coriaceis ovato-deltoideis circiter 1 mm. longis; floribus interdum sessilibus in axillis interdum gracile pedicellatis, basi bibracteolatis, juvenilibus solis visis, sub anthesi ut videtur circiter 5 mm. diametro; sepalis deltoideo-ovatis, 1.1–1.3 mm. longis, 1.5–1.8 mm. latis, apice obtusis, margine minutissime ciliolatis; petalis carnosis concavis suborbicularibus, 2–2.3 mm. longis et latis, apice rotundatis, basi ad 0.8–1 mm. angustatis, extra minutissime puberulis vel glabris; disco inconspicuo carnoso in labia 3 sacciformia staminigera interruptim laxato; staminibus 3, filamentis ligulatis, antheris transversaliter ellipsoideis circiter 0.5 mm. longis et 0.7 mm. latis, per rimas horizontales extrorsas dehiscentibus; ovario carnoso subgloboso sub anthesi ut videtur circiter 2 mm. diametro; loculis 3 stigmatibus alternatis ut videtur 6-ovulatis; stigmatibus 3 summo ovarii radiatim omnino adnatis circiter 0.7 mm. longis staminibus oppositis.

Type, *Krukoff 8760*, collected in Oct.–Dec., 1936, in high forest on terra firma, basin of Creek Belem, Municipality São Paulo de Olivença, basin of Rio Solimoes, Amazonas. It is a very distinct species of Section I of Peyritsch (*Kippistia* Miers), characterized by large conspicuously nerved leaves and lax few-flowered corymbose inflorescences. From *S. podostemma* Sandwith and *S. minutiflora* (above described), apparently its closest allies, the new species differs by its proportionately narrower leaves and by the form of its inflorescence, which is several-pedunculate from the base, fewer-flowered, and only once or twice dichotomously branched.

7. **Salacia Krukovii** sp. nov. Frutex scandens ubique glaber; ramulis fuscis subteretibus dense et conspicue lenticellatis; foliis oppositis, petiolis gracilibus supra canaliculatis 7–13 mm. longis, laminis tenuiter coriaceis siccitate fuscis elliptico-oblongis, 10–15 cm. longis, 3–4.5 cm. latis, saepe leviter falcatis, basi acutis vel attenuatis et petiolo decurrentibus, apice acuminatis (acumine angusto 10–15 mm. longo obtuso), margine integris saepe conspicue revolutis, costa utrinque prominente, nervis lateralibus utroque 6–9 arcuato-adscendentibus utrinque prominulis, venulis supra obscuris subtus reticulatis

minute prominulis; inflorescentiis axillaribus rigidis 1.5–2.5 cm. longis, a basi dichotome multidivisis, ramulis crassis ad nodos bibracteolatis, bracteolis coriaceis late ovatis ad 0.4 mm. longis; floribus sessilibus plerumque 2–4 summo pedunculorum ultimorum congestis; sepalis deltoideis, 0.5–0.7 mm. longis, 0.7–1 mm. latis, basi obtusis; petalis tenuiter carnosis obovato-oblongis, 1.4–1.6 mm. longis, 0.8–1 mm. latis, apice rotundatis, basi angustatis, margine integris; disco inconspicuo carnoso in labia 3 sacciformia staminigera circiter 0.2 mm. alta et 0.5 mm. lata interruptim laxato; staminibus 3, filamentis ligulatis brevissimis, antheris transversaliter oblongis circiter 0.25 mm. longis et 0.4 mm. latis, per rimas horizontales extrorsas dehiscentibus; ovario depresso-subgloboso sub anthesi circiter 0.8 mm. diametro; loculis 3 ut videtur 4-ovulatis; stigmatibus 3 sessilibus divaricatis complanatis bilobatis circiter 0.2 mm. longis staminibus oppositis.

Type, *Krukoff 8817*, collected Oct.–Dec., 1936, in high forest on terra firma in basin of Creek Belem, Municipality São Paulo de Olivença, basin of Rio Solimoes, Amazonas. *S. Krukovii* falls into Section I or Section II of Peyritsch (*Kippistia* or *Amphizoma* of Miers), having certain characters in common with each. The disk is very similar to that of *Kippistia*, but the stigmas are broad and lobed rather than depressed-linear. *Amphizoma*, with which the new species agrees as to stigmas, has an essentially free and not discontinuous disk and a noticeable style. Thus the new species seems to break down some of the distinctions between the two groups. In foliage *S. Krukovii* resembles *S. congestiflora* (below described), from which it differs by its less conspicuous venation, its simpler, less spreading, and fewer-flowered inflorescence, and by disk and stigma characters.

8. **Salacia divaricata** sp. nov. Frutex scandens ubique praeter petala glaber; ramulis gracilibus juventute fusco-olivaceis complanatis demum fuscis teretibus rugosis; foliis oppositis, petiolis gracilibus rugosis supra canaliculatis 10–15 mm. longis, laminis chartaceis siccitate viridibus late ellipticis, 12–14 cm. longis, 5.5–8.5 cm. latis, basi obtusis et petiolo decurrentibus, apice breviter cuspidatis (acumine lato abrupto 5–8 mm. longo obtuso), margine leviter revolutis et undulato-crenatis (dentibus 1 vel 2 per centimetrum), costa utrinque prominente, nervis lateralibus utroque 8–11 patulis prope margines adscendentibus et anastomosantibus utrinque valde prominulis, venulis reticulatis utrinque plus minusve prominulis; inflorescentiis axillaribus 6–8 cm. longis, breviter (1–2 cm.) pedunculatis, dichotome et divaricatim multidivisis, ramulis rectis ad nodos bibracteolatis, bracteolis deltoideis ad 1 mm. longis; floribus sessilibus vel brevissime pedicellatis; sepalis ovatis, circiter 0.7 mm. longis et 0.9 mm. latis, apice rotundatis, marginem versus membranaceis, margine erosulis vel breviter fimbriatis; petalis submembranaceis obovatis, 1.3–1.5 mm. longis et latis, extra distaliter minute fusco-crispato-pilosis, apice

rotundatis, margine integris; disco inconspicuo carnoso in labia 3 sacciformia staminigera circiter 0.1 mm. alta et 0.5 mm. lata interruptim laxato; staminibus 3 patentibus, filamentis carnosis circiter 0.4 mm. longis apice leviter incrassatis, antheris transversaliter ellipsoideis circiter 0.15 mm. longis et 0.2 mm. latis, per rimas horizontales extrorsas dehiscentibus; ovario breviter trigono-cylindrico carnoso sub anthesi circiter 0.8 mm. diametro, summo complanato; loculis 3 stigmatibus alternatis 2-ovulatis; stigmatibus 3 sessilibus complanatis bilobatis staminibus oppositis.

Type, *Krukoff 6351*, collected Sept. 27, 1934, on low terra firma near Tres Casas, Municipality Humayta, basir of Rio Madeira, Amazonas. Like the preceding (*S. Krukovii*), *S. divaricata* shares certain essential floral characters with both *Kippistia* and *Amphizoma*. The two species are quite similar as regards the essential arrangements of disk, stamen, and stigma characters, but differ notably in leaf proportions, venation, and margins, as well as in shape and size of the inflorescence and the presence of pubescence on the petals of the present species.

9. Salacia anomala (Miers) Peyr. in Mart. Fl. Bras. **11** (1): 144. 1878. Basins of Rio Negro, Rio Madeira, and Rio Purus.

10. Salacia laxiflora (Benth.) Peyr. in Mart. Fl. Bras. **11** (1): 145. 1878. Lower Amazon region.

11. Salacia Martiana (Miers) Peyr. in Mart. Fl. Bras. **11** (1): 146. 1878. Amazon and Solimoes regions.

12. **Salacia congestiflora** sp. nov. Frutex scandens ubique glaber; ramulis cinereis obscure dense lenticellatis teretibus juventute plus minusve complanatis; foliis oppositis, petiolis rugosis supra canaliculatis 9–14 mm. longis, laminis chartaceis vel tenuiter coriaceis siccitate fusco-viridibus ellipticis vel elliptico-oblongis, 10–15 cm. longis, 4–6.5 cm. latis, basi obtusis vel acutis vel subattenuatis, apice breviter cuspidatis (acumine obtuso vel saepe apiculato), margine integris et leviter revolutis, costa supra acute elevata subtus prominente, nervis lateralibus utroque 9–13 erecto-patentibus prope margines anastomosantibus utrinque valde prominulis, venulis manifeste reticulatis utrinque prominulis; inflorescentiis axillaribus compactis 1–2.5 cm. longis et latis, fere a basi dichotome multidivisis, ramulis crassis cum bracteis pedicellis calycibusque saepe farinoso-ceriferis; bracteis et bracteolis ovato-deltoideis 0.3–0.5 mm. longis; floribus in ramulis ultimis parvis, sub anthesi expansis 3.2–3.7 mm. diametro, breviter (0.5–1.3 mm.) pedicellatis; sepalis deltoideis, 0.4–0.5 mm. longis, 0.6–0.8 mm. latis, apice obtusis vel subacutis, margine integris vel erosulis; petalis tenuiter carnosis oblongis, 1.4–1.8 mm. longis, 0.8–1.3 mm. latis, apice rotundatis vel obtusis, basi leviter angustatis, margine erosulis, utrinque minutissime intra saepe densissime tuberculatis; disco tenuiter carnoso annulari 0.15–0.3 mm. alto; staminibus 3, filamentis ligulatis

suberectis 0.4–0.8 mm. longis, antheris transversaliter oblongis 0.3–0.5 mm. latis, per rimas horizontales extrorsas dehiscentibus; ovario depresso-subgloboso sub anthesi circiter 0.5 mm. diametro; loculis 3 stigmatibus alternatis 4-ovulatis; stylo carnoso circiter 0.2 mm. longo, stigmatibus 3 carnosis deltoideis patulis integris staminibus oppositis circiter 0.2 mm. longis.

Type, *Krukoff 8297*, collected Sept.–Oct., 1936, on terra firma near Palmares, Municipality São Paulo de Olivença, basin of Rio Solimoes, Amazonas. Another collection is: Territory Acre: near mouth of Rio Macauhan (tributary of Rico Yaco), basin of Rio Purus, *Krukoff 5613.* It belongs in Peyritsch's Section II (*Amphizoma* Miers), but disagrees with that concept in the following characters: (1) ovary 3- rather than 6-locular, (2) stigmas entire rather than lobed. *S. congestiflora* is a close relative of *S. Martiana* (Miers) Peyr., from which it differs by the above-mentioned characters and also by its short inconspicuous disk and its more compact inflorescence with shorter pedicels.

13. SALACIA ATTENUATA (Miers) Peyr. in Mart. Fl. Bras. **11** (1): 149. 1878. Basins of Rio Negro, Rio Solimoes, and probably Rio Madeira.

14. SALACIA CORYMBOSA Huber, Bol. Mus. Goeldi **4**: 580. 1906. Basin of Rio Ucayali, Peru.

15. SALACIA MAURITIOIDES A. C. Smith, Bull. Torrey Club **60**: 364. 1933. Northern Matto Grosso, Rio Machado region.

16. **Salacia cylindrocarpa** sp. nov. Frutex scandens ubique glaber; ramulis gracilibus juventute olivaceis complanatis mox siccitate cinereis subteretibus interdum dense lenticellatis; foliis oppositis, petiolis rugosis supra profunde canaliculatis 10–16 mm. longis, laminis chartaceis siccitate fusco-olivaceis anguste oblongo-ellipticis, 15–23 cm. longis, 4–7 cm. latis, basi attenuatis et petiolo decurrentibus, apice acuminatis (acumine 8–13 mm. longo minute apiculato), margine integris et leviter revolutis, costa utrinque prominente, nervis lateralibus utroque 5–7 arcuato-adscendentibus utrinque valde prominulis, venulis copiose et conspicue reticulatis utrinque prominulis; inflorescentiis axillaribus laxis 7–13 cm. longis, pedunculo ramulisque gracilibus; pedunculo ad 9 cm. longo, ramulis secundariis laxe divaricatis paucifloris apicem versus subdichotome paucidivisis; bracteolis submembranaceis oblongo-deltoideis ad 0.7 mm. longis margine erosulis; pedicellis gracilibus sub anthesi 6–10 mm. longis, floribus expansis 6–7 mm. diametro; sepalis ovato-deltoideis vel obovatis, 0.7–1.2 mm. longis, 1.3–1.8 mm. latis, apice rotundatis, marginem versus membranaceis, margine erosulis vel breviter fimbriatis; petalis tenuiter carnosis vel submembranaceis obovatis, 2.8–3.5 mm. longis et latis, obscure nervatis, apice rotundatis, margine integris et leviter revolutis, basi ad 0.8 mm. conspicue angustatis; disco tenuiter carnoso annulari breviter cylindrico, 0.2–0.3 mm. alto, 1.2–1.4 mm. diametro; staminibus 3 erecto-

patentibus, filamentis ligulatis 0.6–0.7 mm. longis, antheris transversaliter ellipsoideis circiter 0.15 mm. longis et 0.3 mm. latis, loculis leviter divergentibus per rimas horizontales apicales dehiscentibus; ovario in disco immerso, loculis 3, 8(vel 6?)-ovulatis; stylo carnoso gracile conico circiter 0.3 mm. longo, stigmatibus obscuris; drupis (in specimine nostro) geminatis ad apicem ramulorum lignosorum, pedicellis crassis cylindricis ad 18 mm. longis et diametro textura fructibus similibus; drupis maximis indehiscentibus elongato-cylindricis leviter trigonis, ad 11 cm. longis et 4.5 cm. diametro, basi rotundatis, apice obtuse breviter cuspidatis, trilocularibus, dissepimentis demum evanidis; pericarpio duro 2.5–3 mm. crasso extra minute rugoso; seminibus congestis circiter 12–20 angulato-ovatis, extra pulpam involutis, ad 25 mm. longis et 18 mm. latis; testa tenuiter coriacea, cotyledonibus 2 ad 17 mm. longis et 10 mm. latis.

Type, *Krukoff 4559*, collected May 22, 1933, on terra firma near Paranagua, Municipality Teffe, basin of Rio Jurua, Amazonas. On the basis of its flower characters, the new species falls into Peyritsch's Section III (*Tontelea* of Miers), in which it is readily distinguished by foliage and inflorescence characters and by its obscure stigmas. In Miers' treatment it would perhaps be better placed in the genus *Clercia*, but Peyritsch has distributed the eight species there discussed in other sections of *Salacia*. The fruit of *S. cylindrocarpa* is quite unique among the species known to me, and if this character proves to be of basic importance the new species may be found to represent a distinct section.

17. **Salacia nectandrifolia** sp. nov. Frutex scandens ubique praeter sepala glaber; ramulis fuscis subteretibus obscure lenticellatis; foliis oppositis, petiolis crassis rugosis supra canaliculatis 10–13 mm. longis, laminis coriaceis siccitate olivaceis utrinque planis ellipticis vel elliptico-oblongis, 12–18 cm. longis, 5.5–8 cm. latis, basi obtusis et petiolo decurrentibus, apice ut videtur obtuse breviter cuspidatis, margine integris et leviter revolutis, costa utrinque prominente, nervis lateralibus utroque 6–8 adscendentibus utrinque valde prominulis, venulis obscuris vel supra interdum prominulis; inflorescentiis axillaribus 4–6 cm. longis multifloris fere ad basin dichotome multidivisis vel breviter (ad 2 cm.) pedunculatis; bracteis et bracteolis deltoideis 0.4–1.2 mm. longis; floribus sub anthesi expansis 2.2–2.5 mm. diametro, breviter (0.4–0.9 mm.) pedicellatis; sepalis oblongis subacutis, 1–1.2 mm. longis, 0.5–0.7 mm. latis, extra glabris, intra distaliter et margine conspicue pilosis; petalis tenuiter carnosis oblongis magnitudine sepalis aequalibus, apice obtusis, margine minute fimbriatis; disco tenuiter carnoso erecto annulari breviter tubuloso, 0.2–0.3 mm. alto, 0.7–0.8 mm. diametro; staminibus 3 erectis, filamentis ligulatis 0.5–0.6 mm. longis; antheris transversaliter oblongis circiter 0.15 mm. longis et 0.2 mm. latis, per rimas horizontales terminales dehiscentibus; ovario breviter conico basi ad discum adnato; loculis 3, ovulis 2 collateralibus; stylo gracile conico circiter 0.3 mm. longo, stigmatibus obscuris.

Type, *Krukoff 8788*, collected Oct.–Dec., 1936, in high forest on terra firma in basin of creek Belem, Municipality São Paulo de Olivença, basin of Rio Solimoes, Amazonas. Due to the fact that more or less parallel series of floral variations exist both in *Salacia* and *Hippocratea*, the exact position of the present species is uncertain, although the fact that the ovary is strictly round rather than trigonous in cross-section indicates that the fruit will not develop as in *Hippocratea*. In *Salacia*, the new species falls into Peyritsch's Section III (*Tontelea* of Miers), in which it is readily distinguished by its leaf texture, its obscure stigmas, and the ciliate or pilose character of its small petals and sepals. If sought in *Hippocratea*, the new species would fall into Section IV of Peyritsch (*Cuervea* Miers), but here it is almost certainly out of place.

18. **Salacia petiolata** sp. nov. Frutex demum scandens ubique glaber; ramulis fusco-cinereis subteretibus ad nodos incrassatis parce lenticellatis; foliis oppositis vel suboppositis, petiolis gracilibus rugosis supra canaliculatis 13–25 mm. longis, laminis chartaceis utrinque minute rugulosis siccitate fuscis vel fusco-olivaceis elliptico-oblongis, 13–21 cm. longis, 5–10 cm. latis, basi attenuatis vel interdum acutis et petiolo decurrentibus apice breviter acuminatis (acumine 5–10 mm. longo obtuso), margine integris et leviter revolutis, costa utrinque prominente, nervis lateralibus utroque 7–9 arcuato-adscendentibus supra prominulis vel leviter impressis subtus elevatis, venulis supra immersis vel subobscuris subtus leviter prominulis vel interdum obsoletis; inflorescentiis axillaribus vel e ramulis infra folia orientibus quam petiolis plerumque brevioribus, breviter (ad 2 mm.) pedunculatis, dichotome multidivisis; bracteis et bracteolis deltoideis 0.4–0.7 mm. longis margine erosis; pedicellis ad 0.5 mm. longis; floribus sub anthesi expansis circiter 4 mm. diametro; sepalis ovato-oblongis circiter 0.7 mm. longis et 0.9 mm. latis, apice rotundatis, margine erosulis; petalis submembranaceis oblongis, 1.5–1.8 mm. longis, circiter 1.1 mm. latis, apice rotundatis, margine integris; disco tenuiter carnoso erecto annulari breviter tubuloso, circiter 0.3 mm. alto et 1.1 mm. diametro; staminibus 3 reflexis, filamentis carnosis ligulatis 0.9–1.1 mm. longis, antheris transversaliter oblongis circiter 0.2 mm. longis et 0.5 mm. latis, per rimas horizontales extrorsas dehiscentibus; ovario trigono-subgloboso sub anthesi circiter 0.6 mm. diametro; stylo carnoso circiter 0.3 mm. longo truncato vel apice obscure trigono; fructibus immaturis subglobosis ad 2 cm. diametro, pedicellis crassis (ad 7 mm. diametro), pericarpio coriaceo extra densissime cinereo-lenticellato.

Type, *Krukoff 5141*, collected June 30, 1933, on terra firma near mouth of Rio Embira (tributary of Rio Tarauaca), basin of Rio Jurua, Amazonas. The fruit described above is from *Krukoff 4755*, from the type locality, which probably belongs here but which differs from the type by its somewhat broader and less conspicuously attenuate-based leaves.

Another specimen which may belong here is *Cardenas 1763*, from Rurrenabaque, basin of Rio Beni, Bolivia; this has an obovoid fruit 4 cm. long with a rugulose elenticellate pericarp, and has smooth rather than rugulose leaves.

Like the preceding (*S. nectandrifolia*), the new species probably belongs in Peyritsch's Section III (*Tontelea* of Miers), but has obscure stigmas, an unusual feature in this section as previously constituted. *S. petiolata* is separable from *S. nectandrifolia* by its long petioles, attenuate leaf bases, rugulose leaf surfaces, and glabrous sepals.

19. Salacia Colasi R. Ben. Bull. Soc. Bot. France **80:** 335. 1933. Vicinity of Iquitos, Peru.

20. Salacia dulcis Benth. in Hook. Kew Journ. **4:** 9. 1852. Basins of Rio Negro, Rio Solimoes, and Rio Madeira.

21. Salacia laevigata DC. Prodr. **1:** 570. 1824. Peyritsch has reduced several of Miers' species to this, and a critical evaluation of the complex must await further study. In the broad sense, the species occurs in the lower Amazon, Negro, and Madeira regions.

22. Salacia amazonica Loes. Verh. Bot. Ver. Brand. **48:** 179. 1907. Basin of Rio Madeira. From the description this is hardly separable from the preceding.

23. Salacia Ulei Loes. Verh. Bot. Ver. Brand. **48:** 178. 1907. Basin of Rio Jurua.

24. Salacia obovata (Rich.) Peyr. in Mart. Fl. Bras. **11** (1): 154. 1878. Basins of Rio Solimoes and Rio Madeira. It remains to be seen whether or not Peyritsch's variety *amazonica* is conspecific with typical Guiana material.

25. **Salacia acreana** sp. nov. Frutex scandens ubique glaber; ramulis crassissimis 8–13 mm. diametro juventute olivaceis complanatis mox cinereis subteretibus parce lenticellatis; foliis oppositis, petiolis crassis (5 mm. diametro) rugosissimis supra canaliculatis 3–3.5 cm. longis, laminis crassissime coriaceis siccitate fusco-viridibus utrinque rugosis oblongis vel ovato-oblongis, 40–50 cm. longis, 17–20 cm. latis, basi obtusis vel subtruncatis, margine anguste revolutis integris vel leviter undulatis, costa supra acute prominente subtus crassa prominentissima, nervis lateralibus utroque 14–16 validis rectis erecto-patentibus supra subplanis vel leviter insculptis subtus prominentibus, venulis immersis vel inconspicue reticulatis et leviter depressis; paniculis axillaribus vel e ramulis defoliatis orientibus multifloris, 7–9 cm. longis, 5–7 cm. latis, pedunculo brevi, rhachide tereti crassa ad 6 mm. diametro, ramulis primariis 7–12 alternatis dichotome vel saepe alternatim multiramosis; bracteis et bracteolis coriaceis ovato-deltoideis minutis; pedicellis 1.3–1.5

mm. longis; floribus sub anthesi (petalis erecto-patentibus) 2.2–2.7 mm. diametro; sepalis deltoideis circiter 0.9 mm. longis et 1.4 mm. latis, apice acutis, margine erosulis; petalis tenuiter carnosis oblongis vel obovato-oblongis, 1.5–1.8 mm. longis, 0.9–1.3 mm. latis, intra apicem versus incrassatis et irregulariter transverse valde tuberculatis, apice rotundatis plus minusve patento-reflexis, margine membranaceis et integris; disco carnoso conico-pulvinato 0.4 mm. alto, basi 0.5–0.6 mm. diametro superne angustato, apice lobis 3 deltoideis obtusis circiter 0.1 mm. longis dentato; staminibus 3 intra discum insertis erectis, filamentis carnosis gracilibus circiter 0.7 mm. longis, antheris oblongis circiter 0.15 mm. longis et latis per rimas terminales horizontales dehiscentibus; ovario immerso, cavitate disci occluso, loculis 3, 2-ovulatis; stylo subulato circiter 1mm. longo apice truncato; pedicellis fructiferis crassis 9–12 mm. diametro; drupis maximis indehiscentibus subglobosis maturitate 6–8 cm. diametro siccitate fuscis, pericarpio crasse coriaceo 3–6 mm. crasso minute sed aequabiliter ruguloso; seminibus ut videtur plerumque 3 vel 4 oblongis, siccitate ad 40 mm. longis et 25 mm. latis, in pulpa nidulantibus.

Type, *Krukoff 5423*, collected Aug. 11, 1933, on terra firma near mouth of Rio Macauhan (tributary of Rio Yaco), basin of Rio Purus, Territory Acre. A local name is "Gogo," but probably this applies as well to other species of the genus with large fruits. *S. acreana* is such a remarkably distinct plant as to make comparison with any other described species superfluous. In the shape and texture of the disk, the long filaments, and the tapering style with obsolete stigmas it resembles Peyritsch's Section V (*Thermophila* Miers). It differs from the species of that section by having the inflorescence with a stout rachis and many lateral branches, the flowers comparatively minute, the petals thickened and tuberculate within distally, the disk not expanded at base and dentate at apex, the anther locules connate with apical clefts, and the fruit comparatively very large. In view of these numerous and important differences, as well as others in leaf size and texture, it seems that a new section will be required for this species when the genus has been properly revised.

26. **Salacia caloneura** sp. nov. Frutex scandens ubique glaber; ramulis fuscis striatis subteretibus, ad nodos incrassatis et complanatis, lenticellis parvis dense obtectis; foliis oppositis, petiolis rugosis gracilibus supra profunde canaliculatis 13–17 mm. longis, laminis tenuiter coriaceis siccitate supra viridibus subtus fuscis elliptico-oblongis saepe basin versus complicatis, 8–12 cm. longis, 4–5.5 cm. latis, basi rotundatis vel obtusis, apice breviter acuminatis (acumine ad 5 mm. longo obtuso), margine leviter undulatis vel obscure crenatis, costa utrinque prominente, nervis lateralibus utroque 10–13 prope margines adscendentibus et anastomosantibus utrinque valde prominulis, venulis conspicue reticulatis utrinque prominulis; pedunculo axillari gemmi-

formi, bracteis numerosis coriaceis minutis deltoideis; floribus 3–8 per fasciculum, pedicellis et calycibus dense farinoso-ceriferis; pedicellis gracilibus 4–7 mm. longis; sepalis papyraceis vel siccitate tenuiter coriaceis late reniformi-ovatis, 1.3–1.5 mm. longis, 3–3.5 mm. latis, debile nervatis, apice rotundatis, margine integris; petalis sub anthesi rotatis tenuiter carnosis obovato- vel oblongo-spathulatis, 3–3.5 mm. longis et latis, basi ad 1 mm. angustatis, apice rotundatis, margine integris et scariosis; disco carnoso conico-annulari-pulvinato circiter 1 mm. alto, basi 2.5–3 mm. apice circiter 1.3 mm. diametro, per septa inter stamina ad ovarium adnato; staminibus 3 intra discum insertis, filamentis ligulatis 0.8–1 mm. longis et 0.4 mm. latis, antheris transversaliter oblongis circiter 0.2 mm. longis et 0.5 mm. latis, per rimas horizontales subterminales dehiscentibus; ovario in disco immerso subgloboso, loculis 3 circiter 8-ovulatis, ovulis 2-serialibus; stylo carnoso tenuiter conico 0.4–0.5 mm. longo, stigmatibus obscuris.

Type, *Krukoff 8696*, collected Oct.–Dec., 1936, in high forest on terra firma in basin of Creek Belem, Municipality São Paulo de Olivença, basin of Rio Solimoes, Amazonas. It is a species without close allies, by its fasciculate flowers suggesting *Raddia*, but clearly separable from the species of that section by the shape of its disk, as well as by its leaf shape and texture, its conspicuous secondary nerves, and its broad sepals. Probably it is better placed in Peyritsch's Section V (*Thermophila* Miers), from the species of which it is distinguished by its fasciculate flowers and by the disk being adnate to the ovary by septae, thus forming pockets for the stamens. This form of disk is not otherwise found among the Amazonian species.

27. **Salacia macrantha** sp. nov. Frutex (demum scandens?) ubique glaber ad 6 m. altus; ramulis fuscis rugosis striatis subteretibus parce lenticellatis; foliis oppositis, petiolis crassis (ad 4 mm. diametro) rugosis supra canaliculatis 7–20 mm. longis, laminis coriaceis siccitate supra glaucis subtus fusco-glaucis anguste oblongis vel obovato-oblongis, 15–25 cm. longis, 4.5–8 cm. latis, basi attenuatis petiolo decurrentibus, apice ut videtur breviter et obtuse acuminatis, margine integris et leviter revolutis, costa utrinque acute prominente, nervis lateralibus utroque 7–10 adscendentibus prope margines obscure anastomosantibus supra prominulis vel leviter depressis subtus conspicue elevatis, venulis reticulatis utrinque obscuris vel leviter insculptis; inflorescentiis completis non visis, floribus expansis 26–30 mm. diametro; sepalis tenuiter coriaceis late ovatis, 3–3.5 mm. longis, 3.5–4 mm. latis, apice rotundatis, margine integris et saepe scariosis; petalis papyraceis vel submembranaceis luteis sub anthesi rotatis obovato-oblongis, 12–13 mm. longis, 9–10 mm. latis, debile nervatis, apice rotundatis, margine integris, basi 1–2 mm. disci margine obtectis; disco annulari-pulvinato complanato 6–8 mm. diametro, centrum versus carnoso, margine conspicue complanato et mem-

branaceo; staminibus 3 patulis, filamentis ligulatis 2.4–2.7 mm. longis, basi circiter 1 mm. distaliter 0.5 mm. latis, antheris transversaliter ellipsoideis circiter 0.6 mm. longis et 0.9 mm. latis, per rimas extrosas latas dehiscentibus; ovario carnoso trigono sub anthesi circiter 2 mm. diametro, basi in disco immerso, loculis 3 ut videtur 6-ovulatis; stylo carnoso circiter 0.4 mm. longo apice obscure trigono.

Type, *Krukoff 4547*, collected May 22, 1933, on terra firma near Paranagua, basin of Rio Jurua, Municipality Teffe, Amazonas. Although the present material is incomplete (of the inflorescence only a few detached flowers being available), it is sufficient to indicate that an undescribed species of Peyritsch's Section VI (*Raddia* Miers) is represented. *S. macrantha* is characterized by its remarkably large flowers, which considerably exceed in dimensions those of the related Amazonian species. From these the new species also differs by its leaf texture, color, venation, shape, and attenuate rather than rounded base.

28. **Salacia cauliflora** sp. nov. Frutex scandens ubique glaber; ramulis elongatis gracilibus striatis subteretibus, ad nodos incrassatis, lenticellis parvis hinc inde obtectis; foliis oppositis, petiolis rugosis nigrescentibus supra canaliculatis 5–10 mm. longis, laminis tenuiter coriaceis siccitate fuscis oblongis vel lanceolato-oblongis, 10–15 cm. longis, 3–4.5 cm. latis, basi obtusis vel subacutis, apice cuspidatis vel breviter acuminatis (acumine ad 12 mm. longo saepe calloso-apiculato), margine integris leviter undulatis, costa utrinque prominente, nervis lateralibus utroque 10–12 patulis supra minute impressis subtus inconspicue elevatis vel utrinque obscuris, venulis immersis vel supra leviter impresso-reticulatis; inflorescentiis multifloris glomerulatis e ramis vetustis orientibus, pedunculis congestis, bracteis numerosis coriaceis minutis deltoideis; pedicellis et calycibus parce et decidue farinoso-ceriferis; pedicellis gracilibus sub anthesi 15–20 mm. longis; sepalis tenuiter coriaceis late semiorbiculari-ovatis, apice rotundatis, margine integris scariosis, 2 vel 3 exterioribus 1.4–2 mm. longis et 1.8–2.2 mm. latis, interioribus 2.6–2.7 mm. longis, 3.5–4 mm. latis; petalis sub anthesi rotatis carnosis orbiculari-ovatis, 5–5.5 mm. longis et latis, apice rotundatis, basi ad 1.5 mm. angustatis, margine integris; disco carnoso annulari-pulvinato, basi 3–4 mm. apice 1.5–2 mm. diametro; staminibus 3 reflexis, filamentis ligulatis 1.7–1.9 mm. longis, antheris transversaliter ellipsoideis circiter 0.2 mm. longis et 0.5 mm. latis, per rimas horizontales terminales dehiscentibus; ovario in disco immerso, loculis 3 circiter 8-ovulatis, ovulis 2-serialibus; stylo carnoso brevi conico, stigmatibus obscuris.

Type, *Krukoff 8202*, collected Sept.–Oct., 1936, on terra firma near Palmares, Municipality São Paulo de Olivença, basin of Rio Solimoes, Amazonas. Belonging to Peyritsch's Section VI (*Raddia* Miers), the new species is characterized by its scandent caulifloruos habit and its narrow

and obscurely nerved leaves. These points distinguish it from the allied *S. juruana* Loes. and *S. polyanthomaniaca* Barb. Rodr., both of which also have larger flowers and longer petioles than *S. cauliflora*.

29. SALACIA POLYANTHOMANIACA Barb. Rodr. Vellosia **1**: 15. *pl. 8*. 1888. *Anthodon grandiflorus* Benth. in Hook. Kew Journ. **4**: 10. 1852. *Salacia grandiflora* Peyr. in Mart. Fl. Bras. **11** (1): 157. 1878. Not *S. grandiflora* Kurz (1872).

Although the type of Barbosa Rodrigues' species is not available, there seems little doubt from his description and plate that it is the same as *S. grandiflora* (Benth.) Peyr. Both types are from the vicinity of Manaos; that of Barbosa Rodrigues' is said to be from a liana, that of Bentham's from a tree. The shrubs and slender trees of *Salacia* often become highly scandent, so this character is not to be trusted.

30. **Salacia impressifolia** (Miers) comb. nov. *Raddia impressifolia* Miers, Trans. Linn. Soc. **28**: 392. 1872.

Basin of upper Rio Negro. Peyritsch's reduction of this to the preceding seems unwarranted. However, if the two species should be combined, the present name rather than *S. grandiflora* (Benth.) Peyr. or *S. polyanthomaniaca* Barb. Rodr. must be used.

31. SALACIA JURUANA Loes. Verh. Bot. Ver. Brand. **48**: 181. 1907. Basins of Rio Madeira, Rio Purus, Rio Jurua, and probably Rio Solimoes.

32. SALACIA GIGANTEA Loes. Verh. Bot. Ver. Brand. **48**: 182. 1907. Basin of Rio Jurua.

33. **Salacia solimoesensis** sp. nov. Frutex vel arbor gracilis ad 7 m. alta ubique glabra; ramulis teretibus ad nodos incrassatis, lenticellis parvis parce obtectis; foliis oppositis, petiolis crassis rugosis supra canaliculatis 13–18 mm. longis, laminis coriaceis laevigatis siccitate olivaceis anguste oblongis, 20–27 cm. longis, 5–7 cm. latis, basi rotundatis vel obtusis et petiolo leviter decurrentibus, apice ut videtur breviter obtuse acuminatis, margine integris leviter revolutis, costa utrinque prominente, nervis lateralibus utroque 8–10 arcuato-adscendentibus prope margines obscure anastomosantibus supra paullo elevatis subtus prominulis vel leviter insculptis, venulis immersis vel subtus leviter insculptis; inflorescentiis completis non visis; pedicellis gracilibus sub anthesi 5–7 mm. longis; sepalis oblongis vel deltoideo-ovatis, 1–1.3 mm. longis, circiter 1 mm. latis, apice rotundatis, margine integris; petalis tenuiter carnosis sub anthesi rotatis vel reflexis ovato-oblongis, 2.2–2.6 mm. longis, 2–2.3 mm. latis, apice rotundatis, margine integris, basi ad 0.7–1 mm. angustatis; disco carnoso annulari-pulvinato, circiter 0.5 mm. alto et basi 2 mm. diametro; staminibus 3 suberectis, filamentis ligulatis 0.8–1 mm. longis, antheris transversaliter ellipsoideis circiter 0.15 mm. longis et 0.25 mm. latis, per rimas horizontales terminales dehiscentibus; ovario basi in disco immerso, loculis 3 ut

videtur circiter 4-ovulatis; stylo gracile conico circiter 0.4 mm. longo, stigmatibus obscuris.

Type, *Krukoff 8175*, collected Sept.–Oct., 1936, in high forest on terra firma near Palmares, Municipality São Paulo de Olivença, basin of Rio Solimoes, Amazonas. The specimen at hand is very incomplete and only two flowers are available, but from these and the foliage it is obvious that the species belongs in Peyritsch's Section VI (*Raddia* Miers). It is characterized by its long narrow leaves, which most closely resemble in texture and venation those of *S. juruana* Loes. From this, as well as from *S. polyanthomaniaca* Barb. Rodr. and its allies, the new species is distinguished by its small flowers as well as by leaf proportions.

34. **Salacia cuspidata** sp. nov. Frutex scandens ubique glaber; ramulis teretibus fuscis vel cinereis saepe densissime lenticellatis; foliis oppositis, petiolis crassis rugosis leviter canaliculatis 6–10 mm. longis, laminis tenuiter coriaceis siccitate fusco-viridibus oblongo- vel obovato-ellipticis, 11–18 cm. longis, 4.5–8 cm. latis, basi obtusis vel acutis, apice breviter cuspidatis (acumine abrupto 4–10 mm. longo obtuso), margine integris et leviter revolutis, subtus conspicue nigro-punctatis, costa supra paullo subtus valde prominente, nervis lateralibus utroque 8–11 erecto-patentibus prope margines anastomosantibus supra prominulis subtus valde elevatis, venulis reticulatis utrinque prominulis vel supra plerumque immersis; inflorescentiis axillaribus paniculatis 3–4 cm. longis breviter pedunculatis pauciramosis, ramulis rectis gracilibus alternatim vel apicem versus subdichotome divisis, bracteolis tenuiter coriaceis deltoideis 0.4–1 mm. longis; pedicellis gracilibus rectis sub anthesi ad 5 mm. longis; sepalis tenuiter coriaceis deltoideo-ovatis, 0.9–1.1 mm. longis, circiter 1.3 mm. latis, apice subacutis vel obtusis, marginem versus scariosis, margine subreflexis et integris vel erosulis et saepe brevissime fimbriatis; petalis tenuiter carnosis oblongis, 1.8–2 mm. longis, 1.3–1.5 mm. latis, apice rotundatis, margine erosulis vel minute fimbriatis; disco carnoso annulari-pulvinato, circiter 0.4 mm. alto et 1.8 mm. diametro, margine interiore elevato exteriore complanato; staminibus 3, filamentis ligulatis 0.7–0.9 mm. longis, antheris transversaliter ellipsoideis, circiter 0.2 mm. longis et 0.3 mm. latis, loculis plus minusve divergentibus, per rimas transversales apicales dehiscentibus; ovario subgloboso-trigono sub anthesi circiter 0.8 mm. diametro; loculis 3, 2 (vel 1)-ovulatis; stylo subulato carnoso circiter 0.6 mm. longo, stigmatibus obscuris.

Type, *Krukoff 8415*, collected Sept.–Oct., 1936, on varzea land near Palmares, Municipality São Paulo de Olivença, basin of Rio Solimoes, Amazonas. Another collection from the same locality but growing on terra firma is *Krukoff 8255*. It is a species of Peyritsch's Section VI (*Raddia* Miers), in which its freely branching inflorescence separates it from all described species except *S. paniculata* (Mart.) Peyr. From this

S. cuspidata differs by many minor characters, such as its leaf apex, its smaller and differently shaped petals, its less highly elevated disk, and its fewer ovules.

35. **Salacia gracilis** sp. nov. Frutex (demum scandens?) ubique glaber ad 6 m. altus; ramulis gracilibus juventute purpurascentibus ad nodos complanatis mox stramineis teretibus copiose lenticellatis; foliis oppositis, petiolis anguste alatis vel leviter canaliculatis 3–5 mm. longis, laminis chartaceis vel tenuiter coriaceis siccitate supra fusco-viridibus subtus fuscis, obovato-ellipticis, 10–15 cm. longis 3.5–6 cm. latis, basi attenuatis petiolo decurrentibus, apice breviter acuminatis (acumine 6–10 mm. longo apiculato), margine integris et leviter undulatis, costa utrinque prominente, nervis lateralibus utroque 7–9 prope margine conspicue anastomosantibus utrinque valde prominulis, venulis reticulatis utrinque prominulis; inflorescentiis axillaribus 3–5 cm. longis a basi paucidivisis, ramulis gracilibus, internodiis inferioribus ad 14 mm. longis, bracteolis tenuiter coriaceis oblongo-deltoideis 0.7–1.3 mm. longis; pedicellis gracilibus sub anthesi 8–12 mm. longis; sepalis anguste imbricatis ovato-deltoideis, 1.1–1.3 mm. longis, 1.3–1.7 mm. latis, submembranaceis, obscure nervatis, apice rotundatis, margine anguste recurvatis et minute fimbriatis; petalis sub anthesi rotatis tenuiter carnosis vel submembranaceis spathulato-obovatis, 1.9–2.2 mm. longis et latis, apice rotundatis, margine membranaceis et erosis, basi ad 0.8 mm. angustatis; disco carnoso annulari-pulvinato, circiter 0.2 mm. crasso, 2–2.2 mm. diametro; staminibus 3 (raro 4) patulis, filamentis ligulatis 0.4–0.5 mm. longis, antheris rhomboideis, circiter 0.2 mm. longis et 0.5 mm. latis, per rimas horizontales terminales dehiscentibus; ovario depresso-trigono-subgloboso umbonato, sub anthesi circiter 1 mm. diametro; loculis 3, 2-ovulatis; stylo circiter 0.1 mm. longo apice obscure trigono.

Type, *Krukoff 4762*, collected June 12, 1933, on varzea land near mouth of Rio Embira (tributary of Rio Tarauaca), basin of Rio Jurua, Amazonas. It does not readily fall into any of the recognized groups of *Salacia*, being distinct in the form of its annular-pulvinate disk, which is not at all elevated at the inner margin as in Peyritsch's Section VI (*Raddia* Miers). Nevertheless this section appears to be the best place for the new species; a complete revision of the group may indicate the necessity of additional sections. Like *S. paniculata* (Mart.) Peyr. and *S. cuspidata* (above described), but unlike other species of *Raddia*, *S. gracilis* has a freely branching inflorescence. It is at once distinguished by its disk, short style, few ovules, short petioles, and numerous other features.

NEW YORK BOTANICAL GARDEN

INDEX TO AMERICAN BOTANICAL LITERATURE

The aim of this Index is to include all current botanical literature written by Americans, published in America, or based upon American material; the word America being used in the broadest sense.

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Spore Production in Regnellidium

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(WITH PLATE 5 AND FIFTEEN FIGURES)

The paper by Johnson and Chrysler (1938) dealt with the structure and development of the stem, root, leaf and sporocarp of *Regnellidium diphyllum*. Although this Brazilian plant was discovered by Lindman in 1892, and recognized by him as a new genus of Marsileaceae (Lindman, 1904), only a habit study could be undertaken until properly preserved material was available. The material used in the present instance is the same as in the previous paper, and was fixed in the field through the cooperation of Doctor Rau and Doctor Dutra, whose services have made the present studies possible. Several stains were employed; Delafield's haematoxylin for younger stages, safranin and fast green for ripe spores, iron alum haematoxylin, also the tannic acid-ferric chloride combination proposed by Foster (1934). The last method was found to be especially useful in improving the definition of thin cell walls. Sporocarps of *Marsilea* have been available for comparison, through the kindness of Professor W. E. Manning of Smith College.

DEVELOPMENT OF THE SPORANGIA

The origin of the soral initials, development of the soral ridges arising from these, and submergence of these by overgrowth of surrounding tissues of the young sporocarp, have been described and figured in the previous paper (1938). At the stage shown in figure 52 of the paper just mentioned, each soral receptacle is situated on the side of a narrow cavity

[1] Botanical contribution from the Johns Hopkins University, No. 150.

Most of the slides used in this study and a number of helpful notes concerning them were prepared by the late Doctor Duncan S. Johnson and were made available through Mrs. Johnson after his death on February 16, 1937. The present contribution constitutes a continuation of the study projected by Doctor Johnson.—M.A.C.

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opening to the exterior by a small ventral pore. A series of superficial cells of each receptacle are found to be larger than their neighbors, and each becomes divided by an oblique wall which at its lower edge reaches the base of the superficial cell (fig. 1). Next, another oblique wall, opposite the first, appears, and the apical cell of a megasporangium is established. At a slightly later date the same receptacle gives rise to microsporangia. In figure 32 of Johnson's paper of 1898 is shown a slightly developed acropetal succession in the sporangia on a receptacle, that is, a few of the sporangia nearest the ventral end of the sorus are later in beginning their development. We find also in *Regnellidium* that a group of younger sporangia occur at the ventral end, as determined by an inspection of the sporocytes and also of the tapetum. Thus, in figure 37 the sporangium nearest the dorsal end of the receptacle has sporocytes at metaphase of the first meiotic division, while the tapetum has broken up into the plasmodium; the sporangium at the ventral extremity shows sporocytes recently formed, with tapetum still intact; the two sporangia lying midway have sporocytes in early stages of meiosis. Since in *Regnellidium* the vascular supply enters the receptacle at its dorsal end (fig. 16), there may be significance in this tendency to an acropetal sequence of sporangia. The arrangement of sporangia on the soral receptacle is complicated by the width of the latter and by its raised position above the partition upon which it arises. The rather liberal size of the soral canals, due in turn to the shape of the capsule, and the relatively small number of canals also appear to allow room for the sori to spread, so that the megasporangia come to occupy more than the single row which is characteristic of *Marsilea*, while the microsporangia sit not only along the edges of the receptacle but are also found among the megasporangia (fig. 17). Since the sporangia are of various ages, the arrangement should be regarded as a modification of the gradate condition, tending toward the mixed.

We shall trace first the development of a microsporangium, for this is particularly clear on account of the longer stalk. Stages are shown in figures 2–10, in which it may be seen that about six cells are cut off right and left from the apical cell before the cap cell is formed. Because of the finding by Johnson (1898, p. 136) of a tetrahedral apical cell in the microsporangium of *Marsilea*, it is important to establish the shape of the cell in *Regnellidium*. With figures 4 and 7–10 should be compared figures 2 and 3 which we take to be views at right angles to the previous ones. Figure 5 represents a section taken nearly transverse to the tip of a sporangium. These appear clearly to represent respectively the end, side and top views of a dolabriform (or "zweischneidig") apical cell. One other section is significant; figure 6 shows a transverse cut through a sporangium stalk. A;

"zweischneidig" but not a tetrahedral apical cell could produce a stalk having four rows of cells. From figure 2 it will be noticed that promptly after a segment is cut off from the apical cell a longitudinal anticlinal division occurs; in this way the stalk comes to have four rows of cells. We may then regard as proven that the apical cell belongs to the dolabriform type. It should be added that transverse sections through tips of sporangia have failed to show examples of a triangular cell such as is frequently figured as characteristic of the apical cell in Polypodiaceae. The possibility of occurrence of tetrahedral cells is not denied; moreover it may be that an apical cell can begin dolabriform and later become tetrahedral. There is no constancy in orientation of the sporangia; of the members of a row, some show the end of the wedge-shaped initial, while others present one of the more or less flat faces, e.g., the group of three sporangia shown in figures 2, 3 and 4. In spite of their stalk the microsporangia scarcely reach the level of the top of the rapidly growing megasporangia. The latter (fig. 11) are early to be distinguished by their broad short stalk, a condition brought about by growth in width and also division of the stalk cells.

Tapetum.—After cutting off the cap-cell, the apical cell becomes the archesporial cell; two anticlinal walls are formed in succession, then a periclinal wall (figs. 11, 12). The cells cut off externally by these form what may be called the primary tapetal cells; they divide by anticlinal walls (as does also the cap cell), then by periclinal walls cutting off an external layer of flat cells and leaving an inner layer of cuboidal cells (figs. 14, 18). The flat cells of the outer layer show no more cytoplasm than do the so-called jacket cells which make up the wall of the sporangium, but the cuboidal cells stain rather deeply and have a prominent nucleus. These cells divide actively by mitosis in all three planes to form a true tapetum two to three or even four cells in thickness (fig. 19). The number of layers of cells varies in different parts of a sporangium, being greater in places where a slight cavity is left by the rounding off of the contiguous sporocytes. The tapetal cells do not enlarge, as they do in many plants, but increase the bulk of nutritive material by division. Their width is about 85μ, and their walls are extremely thin, so that boundaries of some of the cells are hard to distinguish, but the nuclei are arranged in rather regular radial rows (fig. 19) and some of the cells may be binucleate through solution of walls. Shortly prior to separation of the sporocytes the walls of the tapetum break down, and the comparatively regular arrangement of the nuclei disappears (fig. 20). The flat cells previously described (see figs. 14, 18–21), however, retain their shape and contents, and appear to function as part of the sporangium wall. Immediately following this phase, alveoli

or vacuoles begin to appear in the outer part of the true tapetum (fig. 20), and at first have a diameter somewhat less than that of tapetal cells. Formation of alveoli spreads to the central part of the tapetal mass, which must now be called a periplasmodium. The boundaries of the vacuoles become so distinct that the mass simulates a tissue (fig. 25), although it may be readily distinguished by its foam structure and an increasing difference in size of the meshes. In the meshes of this vacuolate mass lie the nuclei, in which no further divisions have been seen to occur. The vacuoles of the outer region of the plasmodium increase considerably in size, while the region next the tetrads shows only small vacuoles and few nuclei. The latter begin to accumulate around the now separating members of the tetrads, and the plasmodium invades the intervening spaces (figs. 21, 22), bringing about a dispersal of the tetrads through the sporangial cavity. The activity of the plasmodium in building up the epispore will be considered later.

DEVELOPMENT OF THE MEGASPORES

While the tapetum has undergone the transformation into periplasmodium, the sporogenous region has kept pace. Starting with the primary sporogenous cell left after the primary tapetal cells have been cut off, this cell typically appears to undergo four ordinary divisions resulting in the production of sixteen sporocytes. The frequency of sporangia having an ellipsoidal form with the long axis parallel with that of the receptacle is noticeable. In such sporangia the group of sporocytes consists of four rows of four cells each, the long axis of this group again being parallel to the surface of the receptacle. Miss Marschall (1925) figures the same condition for *Marsilea*. In some cases one or more of the divisions fails to occur; for instance in figure 15 is shown a sporangium in which only thirteen sporocytes are found by a study of serial sections.

Even before the sporocytes round off, and while the tapetum is passing into the alveolar condition, the early phases of meiosis are to be seen. Although the preservation of our material leaves much to be desired for cytological work, the following stages have been observed: leptonema, synizesis (!) diakinesis, metaphase, anaphase and telophase of division I, metaphase and telophase of division II. Especially in the diakensis stage it may be noticed that one pair of chromosomes is definitely longer than any of the others (fig. 36). Miss Marschall (1925) has called attention to this feature of the sporocytes in *Marsilea*, although no figure is provided. The presence of satellites in another chromosome pair is to be seen in figure 36. × and + forms of chiasma are frequent. In a few cases of diakinesis it was possible to make chromosome counts, and from these we tentatively estimate $n=16$. Mitotic figures are plentiful in developing

sporangia, but faulty fixation has resulted in clumping, so that determination of 2n has been impracticable.

As the members of a tetrad separate they are seen to be tetrahedral with the usual triradiate ridges which are retained more or less permanently by the microspores. The potential megaspores however round off, especially one of them in one of the tetrads; this spore increases in size while the other three remain undeveloped although still closely associated with the functional one. This stage was observed only a few times (fig. 23). As yet the wall of the megaspore is very thin and the spore is spherical. The plasmodium has already been described as surrounding each tetrad, with a more or less homogeneous layer next the spores. The tapetal nuclei now appear to cluster around the functional member of the tetrad, leaving the outer part of the plasmodium rather coarsely alveolar (fig. 25). The functional spore now becomes placed near the middle of the sporangium, and the spore-wall increases in thickness, thus beginning the formation of the epispore. At the region where the three non-functional spores lie in contact with the developing one, growth of the megaspore-wall is checked (fig. 24), resulting eventually in production of the curious "papilla." Shrunken remains of one or more of the three abortive members of the tetrad are frequently to be seen at this location, lying in a cup-shaped cavity of the megaspore-wall after this has attained a thickness of 7μ (fig. 24). At this stage the wall gives no hint of the complexity soon to be attained. During these early stages the cytoplasm of the megaspore is scanty, forming a thin lining inside the wall: the nucleus is hard to find, although later it may readily be seen in its final position directly under the thin part of the wall, lying in cytoplasm practically free from starch, although oil globules are present. Ellipsoid starch grains averaging 55×37 appear in the peripheral part of the spore cavity (fig. 29), and increase in numbers as the spore ripens until the whole cavity is filled with the mixture of starch grains and oil globules, imbedded in a small amount of cytoplasm (fig. 33).

Meanwhile much of the material of the plasmodium and abortive spores has been consumed in increasing the thickness of the epispore and in developing the characteristic structure which distinguishes this wall layer. For a considerable period the plasmodial nuclei lie clustered more or less unevenly around the thickening megaspore wall—as many as fifty of them can be counted in a single section, and they present every appearance of being active factors in the important metabolic and structural changes which are going on, but eventually they disappear (no stages have been available for study of this process) and the alveolar region of the plasmodium is converted into wall material. At a late date also occurs the dissolution of the outermost, flat-celled layer of tapetum.

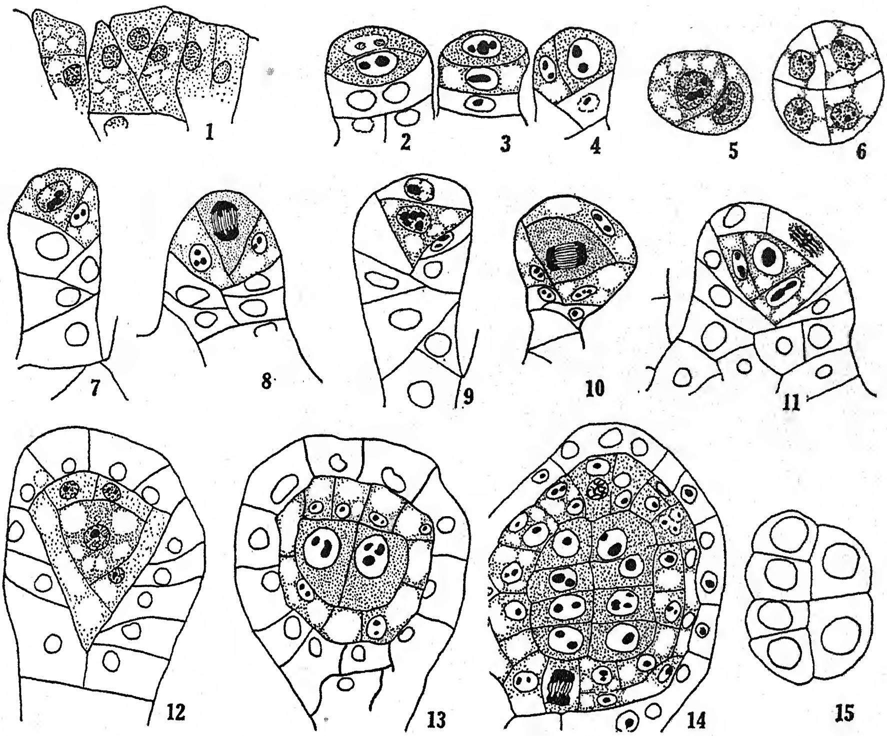
Although normally a single megaspore develops in a sporangium, cases have been observed where two cells of a tetrad develop at least part way into spores. Such a case is represented in figure 26. Another case has been found where three of the members of a tetrad exhibit early stages in differentiation (fig. 27). In another instance two tetrads appear to have begun formation of a megaspore apiece (fig. 28). As many as three sporocytes may begin development and the megaspores may reach a diameter of 50μ. Russow (1872) makes the following reference to *Marsilea:* "in a few cases three vesicles (Blasen) were visible, yet in all cases only one of them developed further." Similar stages were found in *Marsilea* by Shattuck (1910), who regarded them as indicating "sharp rivalry between two or more enlarging potential megaspores." In *Regnellidium*, as in *Marsilea*, "in the end, one centrally placed spore always gains the ascendancy, the others becoming abortive." We have observed that these multiple spores are apt to occur in soral chambers at one end of a sporocarp, suggesting that nutrition may be a factor.

THE MEGASPORE WALL

The mature spore (actually a sporangium, as will be seen later) has a diameter of 0.6 mm, is approximately spherical, creamy white, and finely roughened so as to have a rather dull surface. At one point is a round spot 0.2 mm in diameter, slightly lighter in color, and generally raised into a short nipple-shaped process, the so-called papilla, which represents the thin place in the wall where the three abortive members of the tretrad were situated. When one of these "spores" is placed in a drop of water, an outer membrane is quickly ruptured, and a mucilaginous mass exudes, rapidly swelling due to absorption of water, and surrounding the spore proper. The membrane just mentioned consists of a layer of flat cells, the walls of which consist largely of cellulose, as determined by application of iodine followed by sulphuric acid; it is the wall of the sporangium.

Figure 29 represents a section through a nearly ripe spore, prepared by the paraffin method and therefore showing none of the mucilaginous coating and only fragments of the sporangium wall. At the upper end is to be seen the "papilla," consisting entirely of epispore. Beneath the primary spore-wall lies the ovoidal nucleus imbedded in cytoplasm containing oil globules, but nearly free from starch grains, as previously mentioned. These however form a peripheral layer elsewhere in the spore, and eventually fill the whole cavity. Figure 30 represents a section through the wall of a ripe spore, and in it four layers can readily be distinguished:

1. *Endospore*, the primary cell-wall lying next the cytoplasm. Its thickness is about 3.2μ, and it is continuous under the papilla, where it bulges,



Figs. 1–15: stages in development of sporangia, all ×445.

Fig. 1. Long. sec. through superficial region of a soral ridge. One of the cells has been divided by two oblique walls, forming the apical cell of a sporangium.

Figs. 2–4. Groups of microsporangia, side view, from preparation similar to fig. 17. In fig. 4 the dolabriform apical cell lies in a position at right angles to that of fig. 2 and 3.

Fig. 5. Dolabriform apical cell of microsporangium viewed from above.

Fig. 6. Trans. sec. through stalk of a microsporangium.

Fig. 7. Older microsporangium.

Fig. 8. Sporangium cutting off cap cell.

Fig. 9. Sporangium with archesporial cell.

Fig. 10. Sporangium with archesporial cell dividing to cut off first tapetal cell.

Fig. 11. Megasporangium. Two tapetal cells cut off.

Fig. 12. Tapetal cells cut off, leaving primary sporogenous cell.

Fig. 13. Early stage in division of primary sporogenous cell; tapetum still a single layer.

Fig. 14. Sporocytes in middle, followed by tapetum in which one cell is dividing to form a flat cell of the outer layer and a larger cell of the inner tapetal layer.

Fig. 15. Group of sporocytes, being those lying in one plane out of a set of thirteen. See fig. 17.

Explanation of Plate 5

Figs. 16–30 and 33–37, *Regnellidium*, 31 and 32, *Marsilea*

Fig. 16. Trans. sec. through developing sporocarp, showing two of the soral canals each containing a soral receptacle with its vascular supply. At the lower edge of the figure one of the ventral pores has nearly closed. ×30.

Fig. 17. Portion of a soral receptacle, showing microsporangia among the megasporangia. ×95.

Fig. 18. Sporangium about the age of the one in fig. 13, with differentiation between inner and outer tapetal layers. ×415.

Fig. 19. Sporangium with sporocytes and a tapetum composed of outer layer of flat cells and inner layer which has divided to be about three cells thick. ×350.

Fig. 20. Slightly older sporangium with sporocytes in diakinesis. The walls of the tapetum have broken down and the alveolar plasmodium has replaced the tapetum. ×330.

Fig. 21. End of the second meiotic division. Tapetal nuclei are less numerous in the outer part of plasmodium. ×330.

Fig. 22. Spores are now separated, and plasmodial nuclei have invaded the central area. ×420.

Fig. 23. One spore has begun to enlarge, others are disintegrating. ×390.

Fig. 24. Megaspore has enlarged and wall has thickened except at one place where remains of the tetrad may be seen. Abortive spores lie above these. ×295.

Fig. 25. Older megaspore with tapetal nuclei clustered around it, also the very coarse meshes of the plasmodium. ×260.

Fig. 26. Abnormal tetrad in which two members have partly developed into megaspores. The uneven distribution of the plasmodial nuclei is typical. ×375.

Fig. 27. A case similar to fig. 26; here three members of a tetrad have undergone some development. ×375.

Fig. 28. Attempt of two tetrads to function in a sporangium. ×270.

Fig. 29. Long. sec. through a nearly mature megaspore. The nucleus is visible below the apical papilla. A thin layer of starch grains lies against the primary wall of the spore. ×75.

Fig. 30. Sec. through wall of the megaspore shown in fig. 29. The layer of starch grains is followed by a thin layer of cytoplasm (black), next by the endospore (gray), inner layer of epispore (black), prismatic layer, outer or papillar layer. ×270.

Fig. 31. Sec. of wall of megaspore of *Marsilea quadrifolia* for comparison. Poor development of the papillar layer is to be noted. At the right is a portion of the mucilaginous layer. ×270.

Fig. 32. Tangential sec. through prismatic layer of *Marsilea*, showing the interprismatic substance. ×330.

Fig. 33. Apical region of mature megaspore. The cavity of the spore is now filled with starch and oil, and the nucleus lies beneath a slight bulge in the primary wall outside which lies the papilla. The inner epispore stops at the edge of the papilla, but the prismatic layer bends outward to form the papilla. Covering these is the outer layer of epispore, ragged above the papilla. ×130.

Fig. 34. Microspores, with one tetrad surrounded by a common prismatic layer. ×165.

Fig. 35. Older microspores, showing two cases where a prismatic layer surrounds more than one spore, also a prismatic layer surrounding two tetrads. ×160.

Fig. 36. Chromosome pairs visible at one plane of a sporocyte in diakinesis. One large pair occurs at the left. ×1800.

Fig. 37. Long. sec. through a sorus, showing acropetal succession in megasporangia. See text. ×80.

as is seen in the photograph of this region of a ripe spore (fig. 33). Meunier (1888) says that in *Pilularia* this layer consists of almost pure suberin.

2. *Inner layer of epispore* (called by some authors exospore, perispore, perineum; we prefer the first term on account of its drawing attention to the fact that it is laid down externally, namely by the action of the plasmodium). It has a thickness of about 4μ, is closely applied to the endospore, and appears homogeneous. At the edge of the papilla it comes to a stop—the papilla consists of layer 3 alone. It gives no reaction for either cellulose or lignin; left for several hours in solution of chromic acid it dissolves; it stains reddish with sudan IV. These reactions indicate suberin, in spite of no appearance of a high degree of refractive power. The presence of cellulose or other substances may be masked (a useful discussion of this possibility in the case of meristems occurs in Tupper-Carey and Priestley, 1923). This layer may be regarded as a sort of foundation for the next to be described.

3. *Prismatic layer of epispore.* This forms the bulk of the wall, having a thickness of ca 45μ. It presents the appearance of radiating, slightly wavy lines uniting at the external surface of the layer. A section taken tangentially to the spore wall (fig. 32) shows that these wavy lines are really the walls enclosing more or less cylindrical narrow radiating spaces, the so-called prisms. Tangential sections of sufficient thickness show that the outer end of each prism is covered by a short conical cap formed by the inter-prismatic substance, so that the outer surface of the layer (as may be well seen where layer 4 is accidentally pulled away) presents a fine-papillar appearance, the units of which are about 4μ in height and breadth. Whether in the young spore-wall the prisms consisted of gas rather than some liquid or solid is to be doubted. The micro-chemical reactions correspond to those recorded for layer 2, so that the inter-prismatic substance must consist largely of suberin. This layer is continued into the wall of the papilla, where it has about the same structure but less than half the thickness; moreover it is irregularly wrinkled and lobed (not radially folded as in *Pilularia*), so that its full height is not manifest. There is nothing visible between the wall of the papilla and the endospore beneath.

4. *Papillate layer of epispore.* In the partly ripened spore shown in figure 30 this layer is conspicuous, for it stains with fast green and so contrasts strongly with the inner layers, which take a more or less deep stain with safranin. It is readily detachable from layer 3, and then appears as a series of papillae, each about 13.5μ high and 4μ wide, fitting over the ends of the low papillae which make up the surface of layer 3. As the spore ripens, the papillae of layer 4 seem to condense or shorten slightly, but the layer persists, and is distinguished by its reactions,

being insoluble in chromic acid, but responding positively to cellulose tests. At the edge of the papilla layer 4 separates from the prismatic layer, loses its papillate structure and forms a loose, thin membrane of ragged appearance.

Between the papillate layer and the sporangium wall lies a layer probably thicker than any of the others, consisting of a mucilaginous substance which absorbs water to a high degree. A corresponding layer exists in the other genera of the family, and Meunier (l.c.) considers that in *Pilularia* it constitutes the outermost layer of the spore wall. Whether this point of view is adopted for *Regnellidium* appears to us to be determined by the presence or absence of organization in the mucilaginous mass. Until structure of some sort can be demonstrated in the mass, we prefer to think of the papillate layer as the outermost part of the spore.

MICROSPORES

In the microsporangium the primary sporogenous cell undergoes the four successive divisions which have been found in the megasporangium. Each of the sixteen microsporocytes so formed may pass through the meiotic stages with production of four microspores. The total 64 are not always to be found, but generally 50 or more can be counted. The microspore has a diameter of about 40μ, that is, say one-fifteenth that of the megaspore. In shape (fig. 34) it is approximately spherical, but the "papilla" is larger in proportion than in the megaspore. Moreover the triradiate ridge persists more or less, the angle lying under the papilla. A short prickle is sometimes present, projecting into the papilla. The wall layers that can be made out with certainty are the endospore and the prismatic layer of the epispore. The latter has the same papillate pattern as in the megaspore, but the true outer papillate layer (numbered 4) is poorly developed. The thickness of the wall is ca. 10μ, of which the epispore constitutes say two-thirds. The nucleus occupies the same position as in the megaspore, namely, immediately under the papilla, but starch grains are absent. Thus the microspore is a small edition of the megaspore, but a trifle more clumsy in appearance.

Several cases have been observed where the prismatic layer surrounds a tetrad instead of an individual spore. Such a case is illustrated in figure 34. An older stage is represented in figure 35, showing several instances of two or more members of a tetrad lying loose in a layer of epispore. The largest of these probably represents the attempt of an epispore to surround two tetrads. These curious spores lay in one of the soral cavities situated at one end of a capsule, as was found in the case of the megasporangia mentioned earlier. Their occurrence lends support to the view that in the mega-

spore also the epispore is related to a whole tetrad. In *Marsilea*, Russow (1872) observed two, three or four microspores surrounded by a single epispore. Pollen grains more or less similar to these abnormal spores have been observed in *Cichorium* by Wodehouse (1929), who reports that the giant pollen grains are not functional. These observations lead Wodehouse to conclude that although the material of which the exine is composed comes from the tapetum, the power to organize this material into a normal exine resides in the protoplasm of the spore itself. Hence we meet the old question as to whether the plasmodium is made of living protoplasm.

DISCUSSION

Since the structure and development of all three genera of Marsileaceae are now fairly well known, we should be in a position to inquire into the relationships of the family. Of late years most students of the family have followed the lead of Campbell (1904) who proposed to ally Marsileaceae with Schizaeaceae. Bower (1926) has summed up the evidence, reaching the same conclusion. Eames (1936) has materially strengthened the case. Smith (1938) has recently dissented from this view, proposing to relate Marsileaceae with Cyatheaceae.

One of the criteria, order of development of the sporangia, is not well marked in Marsileaceae. On the basis of the appearance of the microsporangium initials on the sides of the receptacular ridge, following the appearance of the megasporangia on top of the ridge, the condition is considered to be gradate. We have called attention to another indication of the gradate condition, which was proposed by Campbell (1905), namely, the sporangia are slightly acropetal upon the soral ridge, with the youngest sporangia at the ventral end. This is especially well shown in *Regnellidium* because the vascular bundle enters the receptacle at its dorsal end (fig. 16, also Johnson and Chrysler, 1938) so that in this genus it is more appropriate to speak of the base and apex of the receptacle than in the case of *Marsilea*, where the vascular bundle enters near the middle. But the situation is complicated by the subsequent appearance of other sporangia among the older ones, so that there is plainly a tendency toward the mixed condition, as is well illustrated by *Regnellidium*. It is of interest to note that Stevens (1911) finds the sporangia of *Anemia* (Schizaeaceae) arise in acropetal succession. In Cyatheaceae the sporangia are reported as gradate, with transitions to mixed.

Concerning the shape of the apical cell of the sporangium, *Regnellidium* presents a dolabriform cell at least in its microsporangium, in contrast with the tetrahedral cell which Johnson (1898) reported for *Marsilea*. Since the leaf of *Marsilea* arises from a cell with two cutting faces (Han-

stein, 1865) and that of *Regnellidium* in the same way (Johnson and Chrysler, 1938), it is not surprising that in at least one genus of the family the sporangium should develop in like manner. The chief interest in the observation lies in the fact that two genera of Schizaeaceae, *Lygodium* and *Schizaea*, possess a dolabriform apical cell in their sporangia (Binford, 1907; Bartoo, 1929), while the Cyatheaceae are said to follow the rule for leptosporangiate ferns.

An unusually thick tapetum, originating from cells cut off from the archesporium, is characteristic of Marsileaceae and Salviniaceae (Kundt, 1911), also of Osmundaceae where however its origin is different. Attention should be drawn to the differentiation shown in the layers, the outermost one in *Regnellidium* being developed as flat, watery cells which persist as a jacket layer long after the inner, true tapetal cells have fused into the plasmodium. Miss Marschall (1925) reports the tapetum of *Marsilea* as consisting of two or three layers, while Meunier's (1888) beautiful figures of *Pilularia* show nothing thicker than a two-layered tapetum. Neither of these writers notes the persistence of the flat-celled layer. *Regnellidium* appears to exceed the other genera in thickness of the true tapetum, reaching three or locally even four layers in addition to the flat layer. The unusual development of the tapetum is no doubt connected with the great thickness of the megaspore wall, and this in turn appears to be specialized in connection with the aquatic habit, for we note a well-developed tapetum also in *Salvinia* (Kundt, 1911). Here however the layer is strictly a single one, with large cells which are for the most part binucleate. The tapetum in Cyatheaceae is stated to be of the regular two-layered type.

In view of the large number of divisions undergone by the tapetal cells of *Regnellidium*, the conspicuous assemblage of nuclei in the plasmodium is understandable. We do not find figures of any heterosporous pteridophyte in which the condition shown in figure 25 is reached. In *Pilularia* Meunier's figures indicate that the nuclei are not so numerous and undergo an earlier dissolution.

The development of a system of vacuoles through absorption of water appears to be related to the problems which arise in an aquatic plant, for Salviniaceae also show this feature.

The spore wall reaches a high degree of specialization in all genera of Marsileaceae. To a lesser extent the statement is true of the other heterosporous pteridophytes, while in the seed plants only the microspore wall is provided with the exine in which the special features are shown. No doubt the problems which are solved by the spores differ in the various groups. Probably one of the most common necessities is that of bringing the megaspore and microspore into close proximity, and it is usual to

"explain" along this line the common occurrence of spines. Such a device was worked out as early as the Carboniferous, witness the spiny exospore of *Bothrodendron* megaspores. Another Paleozoic plant, *Traquaria*, described by Williamson, and represented by sections deposited at the British Museum (Natural History), displays a remarkable exospore formed of interlacing filaments, the tips of which turn outward and render the spore prickly. There is even the appearance of a plasmodium. All of the heterosporous ferns are aquatics, so that the problems to be solved are

TABLE 1

Structure of the megaspore wall

	MARSILEA	REGNELLIDIUM	PILULARIA
Shape of spore	elongated	nearly spherical	nearly spherical
Dimensions	.425×.750 mm (M. vestita—Campbell)	.6 mm	.4 mm (P. globulifera, calc. from Meunier)
Endospore (shape)	elongated	nearly spherical	pear shaped
Inner epispore	thin	thin	much thicker than endo., esp. toward papilla
Prismatic layer	uniform thickness except papilla; there thin	uniform thickness except papilla; about 2× Marsilea	much thickest toward papilla, there thinner
Outer epispore	may be thickest toward papilla; not markedly papillate	uniform thickness, strongly papillate	much the thickest layer, not papillate
Mucilaginous layer	present	present	present
Papilla (apical)	3 radiating ridges (Campbell)	irregularly folded or lobed	longitudinally ridged (Meunier)

different from those in a plant with the habit of *Selaginella*. The slight degree of relationship between the two families of water-ferns is indicated in the pattern of the spore wall quite as plainly as in other parts of the plants; in both *Azolla* and *Salvinia* the megaspore wall is provided with cup-shaped depressions, while in the three genera of Marsileaceae the "prismatic" layer is the distinctive feature. Although these three genera show the same wall layers (endospore, inner epispore, prismatic layer, outer epispore, also mucilaginous layer if this counts as part of the wall), the details are different. Table 1 offers a comparative view, showing that the megaspores of the three genera differ especially in (1) shape and size,

(2) thickness of the inner layer of epispore, (3) localization of a thick region of the prismatic layer and of outer epispore, (4) relative development of the papillate feature of the third layer of epispore, and (5) details of the apical papilla. In general it may be said that it is as easy to distinguish *Marsilea*, *Regnellidium* and *Pilularia* by sections through their megaspores as by their external characters such as number of leaflets. The spore wall of *Marsilea* appears to be less specialized than in the other genera.

As to the forces at play in laying down the prismatic layer, there are as yet very few data. The work of Wodehouse (1934) has made it exceedingly probable that the exine of pollen grains possessing a pitted surface owes this pattern to the deposit of oil droplets on the surface of the growing wall, restricting the activity of the plasmodium to the spaces between these droplets. While this theory may have application in such cases as *Salvinia*, it offers no explanation of the production of radiating canals. Our curiosity regarding the radiating structure has been heightened when we have recalled the frequency of a prismatic layer in widely separated members of the living world, for instance, the prismatic layer of the sporocarp wall in all three genera of Marsileaceae, the similar layer in seed coats of certain Leguminosae (Russow, 1872), the inner layer of the shell in lamellibranchs, the dentine and enamel of the mammalian tooth. Is there possibly an underlying principle in these diverse instances? Strasburger (1882) studied thin sections of the developing wall in *Marsilea* and came to the conclusion that microsomes derived from the plasmodium become applied to the young spore wall in a radial arrangement corresponding to the radial pattern of the interprismatic substance. Recent work on cellulose molecules renders it probable that Strasburger's "microsomes" may soon receive a re-interpretation. As to the prisms, Campbell (1905) speaks of "close-set prismatic rods" in *Marsilea*. Several years earlier, Strasburger (1882) stated that the developing prismatic areas are filled with a weakly refractive liquid, which later gives place to air. He considers that this condition enables the spores to float on water, an idea that has no doubt occurred to others. Sachs (1875) evidently thought the layer to be really prismatic in *Pilularia*, but Meunier (1888), working with fresh material, insists that the radiating appearance is due to cavities filled with gas. Besides functioning as a floating device in the mature condition, it is possible that the immature wall serves a conducting function. The extent to which materials must pass through the spore-wall after the various layers are organized may be realized by an inspection of figure 29. This nearly mature spore contains a rather thin layer of starch grains, and the wall has not attained quite its full thickness, although the prismatic layer

is well developed. It is of course possible that the wall at this stage does not contain enough suberin to prevent passage of carbohydrates, etc., which evidently enter the spore and build up the starch grains and oil globules in quantity to eventually fill the cavity. The apical papilla is probably the most pervious region of the wall, as is indicated by the rapid development of the gametophyte. Perhaps we see here a meaning of the radiating canals or spaces—the so-called prisms. As the spore ripens the chemical nature of the wall may change with deposit of suberin and the wall may assume the character of a floating device.

Concerning the relationships among the three genera of Marsileaceae, there is every reason to consider that *Pilularia* represents reduction stages culminating in *P. minuta*. This is indicated not only by the lack of leaflets but by the small number of soral canals and of sporangia. In *Marsilea* the four leaflets may be regarded as primitive, also the large number of sporocarps (2–20), and perhaps the large number of soral canals (8–10 on each side). The megaspore wall is moreover simplest in this genus, being specialized in one respect in *Regnellidium* and in another in *Pilularia*. On the other hand the venation of the leaves is strictly dichotomous in *Regnellidium*, while frequent anastomoses occur in *Marsilea*. Surely the mucilaginous ring which bears the liberated sori in the latter genus should be regarded as a feature of specialization, absent in the other genera. Moreover the dichotomous plan of venation in the sporocarp is more clearly expressed in *Regnellidium*, probably on account of the location of attachment of stalk to capsule (see Johnson and Chrysler, 1938). This clearly expressed dichotomy extends to the origin of the vascular bundles supplying the sori. Thus it is difficult to reach a conclusion as to which genus comes nearest to the terrestrial ancestor. But the view may be entertained that *Regnellidium* represents an ancient and unprogressive member of the group, showing certain features of reduction, while *Marsilea* is the progressive member which has worked out such devices as the mucilaginous ring and a branching (chorisis?) of the sporocarp. At any rate *Marsilea* has become cosmopolitan and includes over fifty species, while *Regnellidium* is monotypic, a tropical endemic, perhaps relic.

A survey of the new evidence appears to give little reason for departing from the current opinion that the nearest relatives of Marsileaceae are Schizeaceae, in spite of some features suggestive of Cyatheaceae. Probably the most serious drawback to the schizeaceous alliance is the "monosporangiate sorus" of the Schizeaceae. This however may represent a special feature of the modern members of this family which was not present when the Marsileaceae branched off.

SUMMARY

1. The sporangia of *Regnellidium* exhibit a slight acropetal succession on the soral ridge, the base of which is considered to be the dorsal end where the vascular bundle enters.

2. The apical cell of the microsporangium is dolabriform, a feature which is regarded as a point of contact with Schizeaceae.

3. The micro- and mega-sporocytes are normally sixteen in each sporangium. A single megasporocyte ripens only one of its resulting spores, although several sporocytes of a sporangium may begin development, also two or more of the members of a tetrad may make some headway.

4. In the megasporangium the primary tapetum cuts off an external layer consisting of flat watery cells which are notably persistent. The inner cells divide in all three planes to form a 2–4 layered true tapetum, which fuses into a periplasmodium at about the time of separation of the spores. The plasmodium is richly provided with nuclei which appear to be active in building up the epispore.

5. The megaspore wall comprises: (1) endospore, (2) inner layer of epispore, (3) thick "prismatic" layer of epispore, (4) outer layer of epispore, the papillate form of the last being characteristic of the genus, as is also the shape of the apical papilla.

6. An epispore normally forms around each microspore, but occasionally surrounds a whole tetrad or even two tetrads. The microspore possesses a prismatic layer, and an apical papilla with remnants of the triradiate scar.

7. In general the features exhibited by *Regnellidium* are considered to strengthen the case for an alliance with Schizeaceae.

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Studies on Rhizophidium. III. Germination of the Resting Spores

J. S. Karling

(with plate 6)

Rhizophidium is the largest of the rhizidiaceous chytrid genera and at present is reported to include approximately fifty-five species, a large number of which are doubtful or imperfectly known. A survey of the literature shows that resting spores have been found in only twenty-one species and that germination has been seen in but three of these. In the course of a study on members of this genus a saprophytic species was found on dead cells of *Hydrodictyon reticulatum* whose resting spores germinated readily under laboratory conditions. The identity of this species is uncertain, but the shape and size of its zoosporangia are similar to those of *R. sphaerocarpum* and *R. globosum.* Since there are many similar species which will infect dead algal cells and other plant tissues, I hesitate to assign a specific name to the species at hand before a more intensive study of its development, structure, cultural characteristics, host range, etc., has been made.[1]

The mature resting spores are predominantly spherical, 8–15μ in diameter, but slightly oval and ellipsoidal spores, $5\times7\mu$–$10\times14\mu$, also occur. They usually contain a large refractive globule in the center, which may often be more than half as large as the spore itself. The wall is amber to dark brown, smooth or rough, and varies from 2–3.5μ in thickness. The thickening and roughening of the wall can be followed readily in living material, and frequently when two or more spores occur close together, their adjacent walls fuse as the thickening proceeds, as is shown in figures 2 and 7. Figure 2 shows three spores in optical section with their adjacent walls united in the center.

Hyaline empty vesicles have often been found adhering to the sides of the spores, as is shown in figures 5 and 6. Such structures have been interpreted by Scherffel (1925), Couch (1932), and Sparrow (1933, 1935, 1936) as remains of male thalli which have fused with female thalli to form the resting spores. So far, I have not observed such fusion in this species, and the significance of the empty hyaline vesicles remains to be seen.

The resting spores germinated readily under the laboratory conditions of this study. As many as fifteen spores have been found germinating at the same time on a single host cell. The first stages were found five days after the spores were formed, and within fifteen days about 80 per cent had germinated. Subsequent observations have shown that germination is not unusual in the laboratory during the winter and spring months and

[1] The identity of this species and the evidence of sexuality are being investigated at present and will be reported in a subsequent paper.

that no long period of dormancy is necessary. Whether such abundant germination is seasonal or dependent on certain edaphic conditions has not been determined. The *Hydrodictyon* cells on which the resting spores developed had previously been dried, bleached in the sun, stored for a month, and then placed in shallow dishes filled with water from the greenhouse tanks. Heavy infection occurred within four days. The dishes were kept on a table before an east window and thus received several hours of direct sunlight. During the nights the temperature frequently dropped below 30°C., so that the chytrid resting spores were thus subjected to a wide range of temperature during the course of twenty-four hours.

The first visible change preparatory to germination is the development of a small germ pore in the thick brown wall. This pore varies from 1–2.5μ in diameter according to present observations and may be readily overlooked unless seen in profile view (fig. 3). While the development is going on, the refractive globule in the center of the spore begins to change somewhat in shape, particularly on the periphery adjacent to the pore, and as the protoplasm slowly emerges through the pore, this change becomes more apparent. Figure 3 shows an early germination stage with a small, spherical mass of protoplasm growing out of the spore, which may readily be recognized as an incipient zoosporangium. The large refringent globule in the spore appears to have become eroded on its periphery adjacent to the pore, as if it were undergoing fragmentation in that region. Numerous small fragments of refringent material are present underneath the pore as well as in the incipient sporangium, and these seem to have arisen from the larger globule in the spore. The wall of the young developing sporangium at this stage is usually very thin and is scarcely perceptible as such, while the protoplasm may often be quite vacuolate. Later developmental stages are shown in figures 4 and 7B. The incipient sporangia are considerably larger, contain several conspicuous, irregular and spherical refringent bodies, and are enveloped by a delicate but visible hyaline wall.

Explanation of Plate 6

Fig. 1. Small smooth resting spore of *Rhizophidium* sp.

Fig. 2. Three large rough-walled spores in optical section.

Fig. 3. An early stage of germination in which the young sporangium is forming on the outside of the spore.

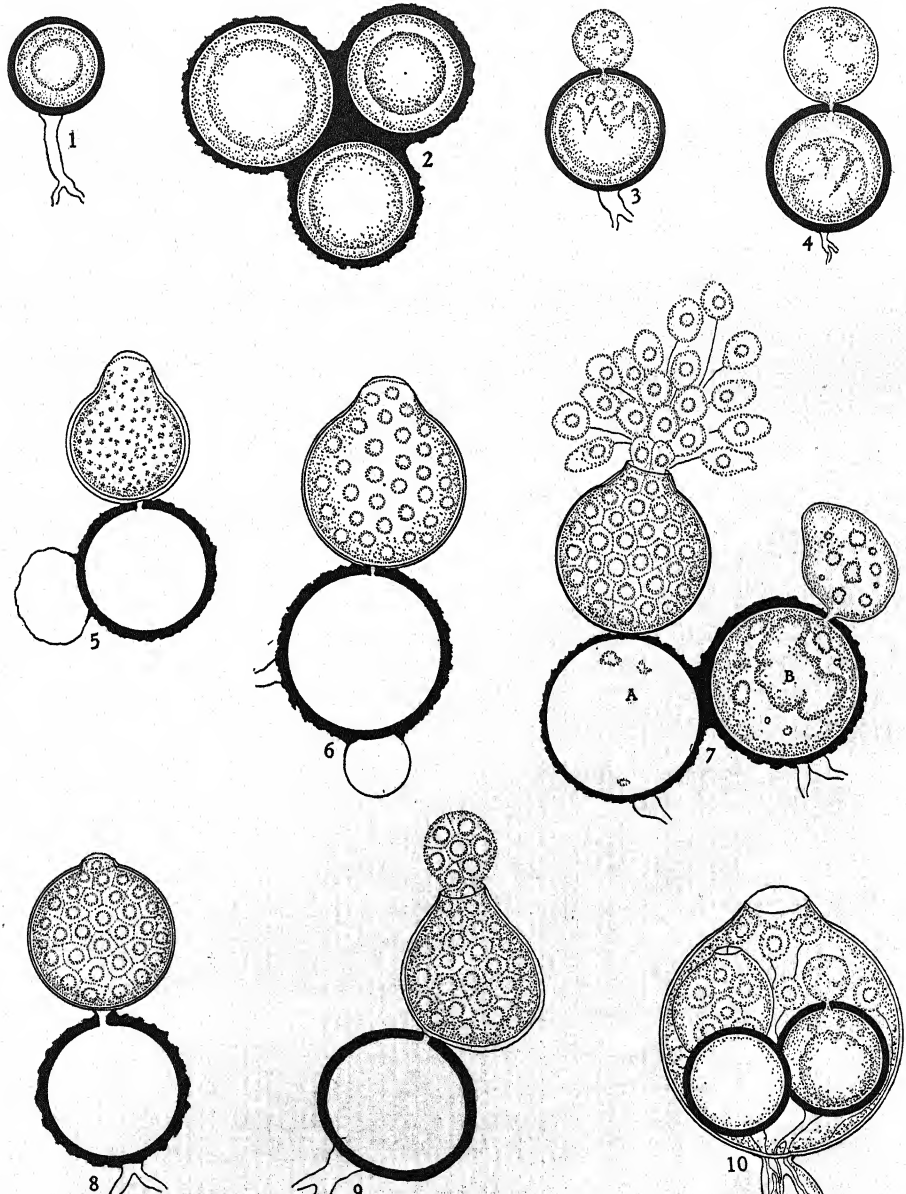
Fig. 4. A later stage.

Fig. 5. Completion of germination; the sporangium has attained its mature size.

Fig. 6 and 8. Stages in maturation and zoosporogenesis.

Fig. 7 and 9. Emergence and dispersal of the zoospores.

Fig. 10. Germination of two resting spores in an old sporangium.



KARLING: RHIZOPHIDIUM

The large globules in the spores have been reduced to about half their original size and become irregular in contour. The remainder of the protoplasm in the spores is highly vacuolate and consists largely of a primordial utricle. Occasionally at this stage the remnant of the large refringent globule may lie shrunken at the side opposite the germ pore.

The incipient zoosporangium continues to grow in size with the slow and gradual movement of the protoplasm out of the resting spore. This movement, however, is not sufficiently rapid to be observed with the oil immersion lens, and the complete development of the zoosporangium may require 8 to 16 hours. In the process of development the large refringent globule usually breaks up entirely, and its material passes out into the sporangium with the result that the resting spore may be completely emptied. Occasionally a few refringent segments may be left behind, as is shown in figure 7A. As development of the sporangium proceeds, the refringent material becomes more and more dispersed, so that by the time the zoosporangium has attained mature size, its protoplasm is somewhat evenly granular and grayish in color (fig. 5). The sporangium shown in this figure, though immature, is fully grown, possesses a well developed apical papilla, and has been delimited from the empty spore by a cross wall. Following this stage, the minute, highly dispersed refractive granules begin to coalesce, until finally a fairly definite number of conspicuous spherical globules are formed, as shown in figure 6. Within a short time the outlines of the zoospores become visible (fig. 8), and eventually the exit papilla deliquesces to emit the swarmspores (figs. 9, 7). The method of emergence and initial behavior of the zoospores are similar to those of the primary evanescent zoosporangia of other species of *Rhizophidium* (Karling, 1938), and it is unnecessary to recount the details here.

The mature sporangia vary from spherical in shape, 8–18μ in diameter, to ellipsoidal, ovoidal or pyriform, 5×7–$10\times18\mu$, and usually possess a single exit papilla. Figure 10 shows an old primary sporangium with two germinating resting spores within. These doubtless developed from zoospores which failed to escape and later germinated into thalli. The resting spore on the right has just begun to germinate, while in the one on the left germination and dehiscence of the sporangium are complete, and have given rise to the zoospores which are swimming about in the large old sporangium. Such structures as are shown in Figure 10 have been observed in three instances.

It is apparent from this description that resting spore germination in *Rhizophidium* sp. is fundamentally similar to that reported for *Polyphagus euglenae* (Nowakowski, 1877b; Wager, 1913), *Rhizidium mycophilum* (Nowakowski, 1877a), *Entophlyctis vaucheriae* (Fisch, 1884), *Chytridium*

Olla (De Bary, 1884), *C. Schenkii* (Sparrow, 1932), *C. lagenaria* (Karling, 1936), *Megachytrium Westonii* (Sparrow, 1933), *Diplophlyctis intestina* (Karling, 1936), and *Rhizidiopsis emmanuelensis* (Sparrow, 1936). The resting spore functions as a prosporangium, giving rise to a relatively thin-walled zoosporangium on its surface.

In *Rhizophidium ovatum*, however, Couch (1935) figures the resting spore or zygote as becoming transformed directly into a zoosporangium and thus giving rise to zoospores as in *Zygorhizidium Willei* (Lowenthal, 1905). Couch is not certain that his species belongs in *Rhizophidium*, and, as he suggests, it may possibly relate to the genus *Phlyctidium*. The same direct method of germination and zoospore formation has been reported by Dangeard (1900) for *R. transversum*, but this species may likewise belong in *Phlyctidium*, since he figures its absorbing system as consisting only of an elongated unbranched filament. It is to be noted in this connection that with the possible exceptions of Couch's and Dangeard's species, germination of the resting spores has never been reported in *Phlyctidium*. In another so-called *Rhizophidium* species, *R. messanensis*, Morini (1896) also figures the resting spores as forming zoospores directly without the development of a zoosporangium on its surface. This species, however, develops an extensive and branched rhizoidal system, so that it cannot be included in *Phlyctidium* as this genus is now recognized. In view of the fact that the main axis of its rhizoidal system is occasionally inflated like an apophysis, it may perhaps relate to *Phlyctochytrium*. If these three species do belong in *Rhizophidium*, it is apparent that two types of resting spores germination occur in this genus.

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Flower Buds and Phylogeny of Dicotyledons

Alfred Gundersen

(with seven figures)

Differences of opinion regarding the classification of the dicotyledons have been many. Nevertheless, certain tendencies or directions of floral evolution have become almost universally recognized, such as those relating to sympetaly, to zygomorphy, to epigyny, to the fusion of carpels, and others. In many cases accepted views are definitely supported by the structure of flower buds. The present study relates largely to placentation.

Petals: from separate to united

Flower buds and flowers in different families are illustrated by Maud H. Purdy in Figure 1. Comparing the bud of *Azalea* (*Rhododendron indicum*), 1 mm. long, with the flower, 30 mm. long, we note that in the bud the separate parts of the corolla are about four-fifths of its total length; in the flower they are only one-third of the length. In *Plumbago capensis* the bud, 1 mm. long, has separate parts about three-fourths the length of the corolla; in the flower, 20 mm. long, they are only one-eighth of its length. In *Forsythia viridissima* the bud, 3 mm. long, has separate parts about three-fourths of its length; the flower, 10 mm. long, has the separate and fused parts about equal. In the bud of *Lonicera fragrantissima*, 3 mm. long, the separate parts are about four-fifths of its length; in the 10 mm. flower the separate and united parts are about equal. These examples might be extended indefinitely. In each case the petals of the sympetalous flower are more nearly separate in the bud than they are in the adult flower. In other words, the growth occurs mainly in the lower, fused part, with the result that in the adult flower we have corolla lobes rather than petals. It is agreed that the upper, divided part of the corolla represents the early stage; the lower, fused part the advanced stage of floral evolution.

Petals: from actinomorphy to zygomorphy

Figure 1 at the same time illustrates the development of zygomorphy. The *Azalea* bud of 1 mm. is practically actinomorphic, in the flower zygomorphy is evident. Likewise in *Lonicera* zygomorphy is much more in evidence in the flower than in the bud. Among the polypetalous families comparatively few are zygomorphic; such are most Leguminosae, Resedaceae, Violaceae, Polygalaceae, Balsaminaceae and others. But in the Sympetalae numerous families are typically zygomorphic. In the flower of Leguminosae one stamen is usually separate from the others, in the young bud they are practically similar to one another. For example, in

the bud of *Clitoria Ternatea*, when less than 1 mm., the ten stamens are nearly alike, the large anthers having hardly any filaments. The development is always toward zygomorphy, never the opposite.

SEPALS: FROM SEPARATE TO UNITED

While much has been written about sympetaly, synsepaly has received little attention. The development of sepals is like that of petals, that is, in synsepalous flowers the separate sepals are more prominent in the bud than in adult flowers. We conclude that polysepaly is the primitive, and synsepaly the derived form. Separate petals occur in a great majority of the dicotyledons, but separate sepals are found in comparatively few families. These are nearly all in three groups: Ranales, Papaverales and Parietales, groups which are also for other reasons suspected of being primitive.

OVARY: FROM SUPERIOR TO INFERIOR

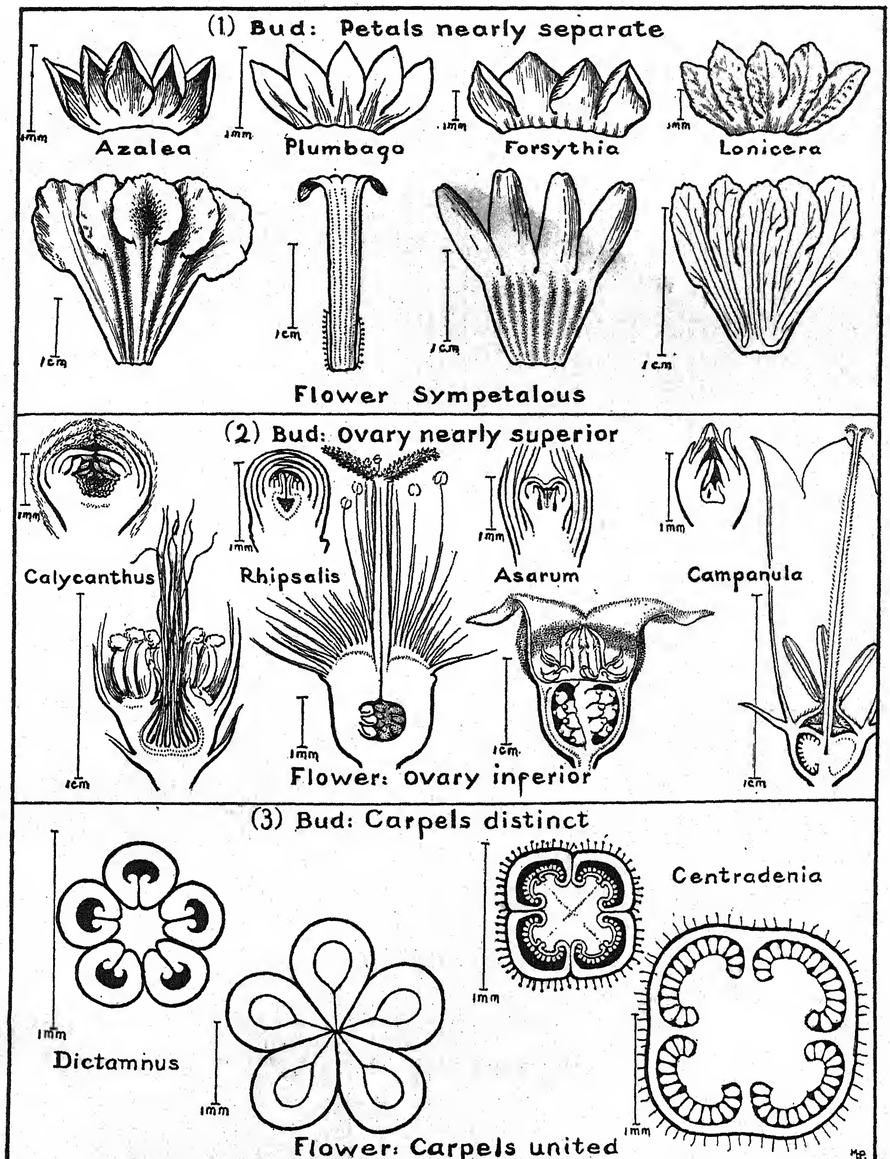
In Figure 2 *Calycanthus fertilis* represents a perigynous flower. In the bud the depth of the ovaries is about one-half the cross-section above them, in the flower the depth is about four times that section. In the bud of *Rhipsalis rhombea* the ovary is approximately on the level of the perianth, but the flower is definitely epigynous. In the bud of *Asarum canadense* the young carpels together with the stamens are raised above the base of the perianth; in the flower there is a definite inferior ovary. In the *Campanula rotundifolia* bud the beginnings of the carpels show similar difference with the adult flower. It appears to be a general fact that in buds of epigynous flowers the ovary is more nearly superior than in the adult form. Epigny is recognized as being more advanced than hypogyny. The greater protection of the ovules must be considered an advantage to their development.

CARPELS: FROM SEPARATE TO UNITED

In Figure 3 the bud of *Dictamnus albus* shows the carpels nearly separate, with a considerable central space. When the diameter has enlarged about three times the carpels are nearly fused. In the bud of *Centradenia floribunda* the carpel lines are distinct, in the flower they are obliterated. Separate and open carpels in the young bud is the usual condition. The style is always very slightly developed in the bud. However, a few adult flowers do have somewhat open ovaries, notably *Reseda*, *Platanus* and Cactaceae.

Separate carpels are usual in the *Magnolia* and *Rosa* groups of families, outside of these they are unusual. But in numerous families we have sepa-

ably be considered as the remains of former separate carpels, analogous to the corolla lobes of Sympetalae. Hallier, Arber and Parkin, Bessey, Wie-



Figs. 1–3. Flower buds and flowers compared.

land (13), Eames (4) and others have presented strong and varied evidence showing that plants with separate carpels should be considered the basal

PLACENTATION: HISTORICAL

From the above illustrations of the principle that ontogeny recapitulates phylogeny, we pass to a subject not so generally agreed upon, namely placentation. The involved changing views as to placentation deal largely with central placentation, the history of which has been outlined by Douglas (3). Occupied with the axial versus appendicular discussion, Payer (8), in 1857 considered *Polygonum*, *Chenopodium* and *Primula* as exhibiting the simplest form. From his drawings, however, numerous examples are seen of flowers with axile placentation which in the bud have open centers similar to those of flowers with parietal placentation. In 1874 Eichler wrote in his *Blütendiagramme* "The whole question of placenta formation deserves a new investigation, both from a developmental and from a systematic-comparative point of view."

Engler wrote in his *Syllabus:* When in a related group there is only parietal placentation, it is not necessary to assume that this is a progression from a many-celled ovary; for as soon as syncarpy arose, either a many-celled or one-celled ovary might develop, according as the carpel margins were more or less bent inward." Diels (2) stated, in 1920, under *Organisationshöhe und Progression der Merkmale:* "Ovary cells as many as the carpels to less than these." These statements together with the placing of *Parietales* so high in the Engler system suggest that parietal placentation is considered to be a derived form. Placentation is not referred to in the list of evolutionary tendencies by Bessey (1914). But the parietal-axile sequence of placentation is accepted by Sprague (9) in his *Classification of Dicotyledons* (1925). Though Hutchinson does not include placentation in his principles of classification in his book *Families of Flowering Plants*, (7), the same year (1926), he stated at the Ithaca Congress: "After syncarpy was attained, the parietal type of placentation generally preceded the axile, basal, or apical types, the axile being the final and most efficient condition." But this principle is given little attention in his system.

PLACENTATION: FROM PARIETAL TO AXILE

The genus *Hypericum* has two kinds of placentation, parietal and axile. *Hypericum gentianoides*, *H. ellipticum* and others have a one-celled ovary with three parietal placentae. In these species the young ovaries have open centers the same as the adult forms. The development of axile placentation of *Hypericum densiflorum* is shown in Figure 4. To the left the ovary is half a millimeter in diameter and shows essentially parietal placentation. In the longitudinal section of the bud we note that at this stage the placentae are fused only at the base. To the right, the ovary, at

a later stage is shown with a diameter about three times larger. Here we have axile placentation; in the longitudinal section we note that only the top part has an opening in the center. *Hypericum perforatum* and other species with axile placentation show similar development. If this is a case where ontogeny recapitulates phylogeny, we must consider the species having parietal placentation to be the primitive ones.

The development in *Theobroma Cacao* (Sterculiaceae) is shown in Figure 5. In the longitudinal section we note the open part above, the fused part below. The open part between the placentae, conspicuous in the bud, gradually disappears in the flower, and we have axile placentation. Figures 6–8 show similar development in Zygophyllaceae (*Peganum harmala*), Hydrangeaceae (*Philadelphus coronarius*), Scrophulariaceae (*Verbascum Thapsus*) and Iridaceae (*Iris pumila*).

In general, the cross-section of young ovaries of flowers with parietal placentation is about the same as in the adult flower. But not so with those having axile placentation. Among the numerous genera which have open centers in the bud may be mentioned *Hibiscus*, *Tilia*, *Gordonia*, *Ruta*, *Ilex*, *Linum* and *Tropaeolum*. In all cases the change or suggestion of change is from parietal to axile placentation, never the reverse. In a number of cases, for example *Shortia*, *Feijoa* and *Myrtus*, the upper part of the ovary has parietal placentation, the lower part axile. The reverse does not occur. Here, as with the petals, we must consider the upper part to represent the primitive condition.

Among Sympetalae parietal placentation is rare, in itself a suggestion that is is a primitive character. Gentianaceae, except *Exacum*, have parietal placentation. But the bud of *Exacum* has at first open center like that of *Gentiana*, axile placentation gradually developing. In the *Natürliche Pflanzenfamilien*, the Gentianaceae begin with *Exacum* because of its axile placentation, but a terminal position would be preferable.

In many families such as Papaveraceae, Cactaceae, Gentianaceae and others, we find numerous small seeds associated with parietal placentation. Many stamens and many small seeds are in general primitive characters. Advanced flowers such as those of Labiatae and Compositae, have few stamens and few seeds or a single seed per flower.

PLACENTATION AND CLASSIFICATION

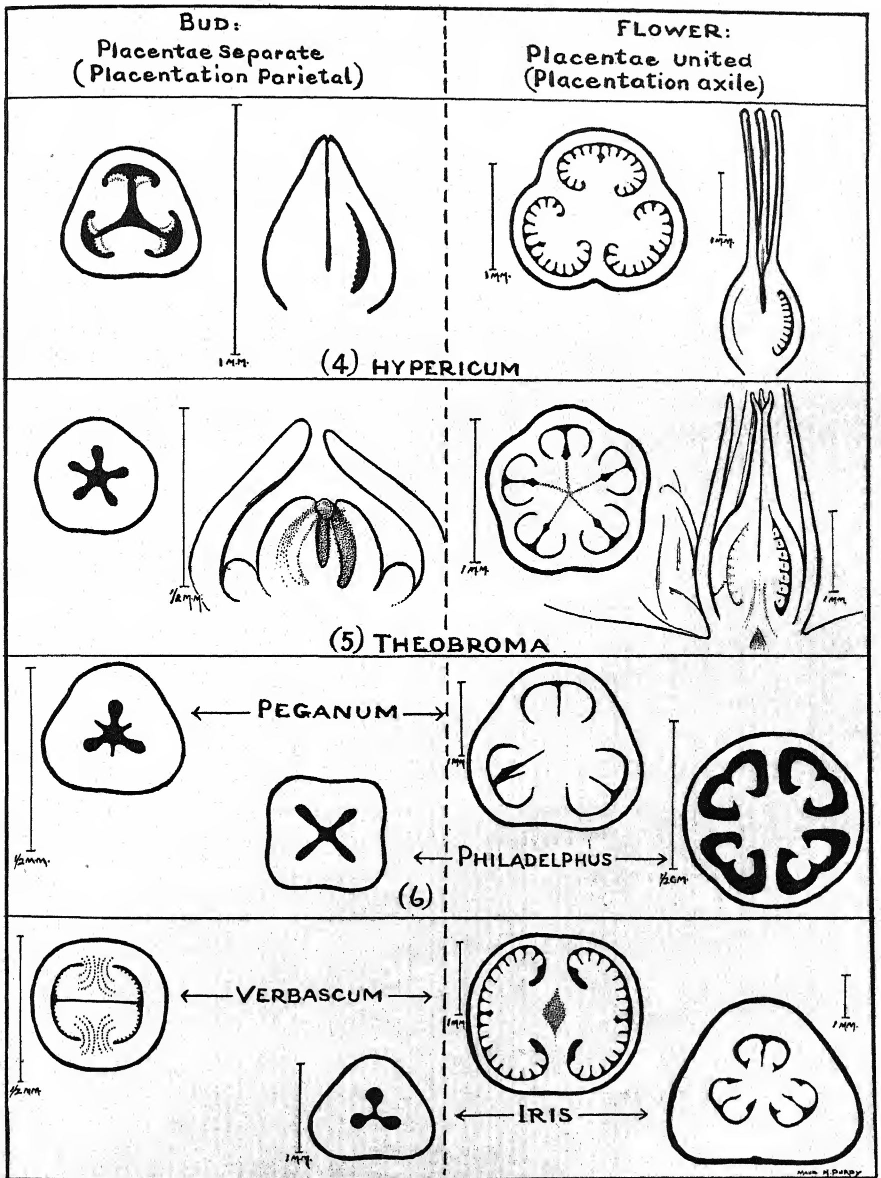
Families of Parietales with spirally arranged flower parts, numerous stamens and other primitive characters connect on the one hand closely with the Ranales of the Engler system, on the other hand with the Papaver group of families. In particular the families Cistaceae and Papaveraceae have many characters in common. In the systems of Jussieu,

DeCandolle, Bentham and Hooker, and Eichler they are near together. But in the Engler system Parietales come between Malvales and Opuntiales. The separation of Parietales from Papaverales is a peculiarity of the Engler system, though Engler also accepted their affinity as seen in his suggestive diagram (5) of 1897. At the same time he wrote that his order Parietales is a complex of groups of different origins which have arrived at a similar morphological state (meaning parietal placentation?). In the later systems of Warming, Wettstein, and Bessey *Cistus* and *Papaver* have again been brought near together, rightly we think. Even Rendle, whose *Classification of Flowering Plants* (9) follows approximately the Engler system, departs from it in this respect and adopts the arrangement *Rhoeadales*, *Sarraceniales*, *Parietales*. Mez wrote in 1926, "Large branches of the dicotyledon system are derived from the region of the Parietales, these stand exceedingly close together." Mez places the *Papaver* group near Parietales. Tippo (12) has made suggestions for the relationships of supposed primitive dicotyledons; axile placentation is almost entirely absent among these families. Wilson (14) points out primitive characters of stamens in Parietales and Malvales. F. H. Taylor (11) stated recently (1938), "Anatomically, Violaceae and Flacourtiaceae (Parietales) exhibit numerous primitive features, whose discovery is definitely interesting in dicotyledons placed high in the Archichlamydeae,"—"in the Engler system" should have been added.

Cactaceae usually have parietal placentation, though *Pereskia* has basal ovules like *Tamarix*. The resemblance of flowers of Cactaceae and Nymphaeaceae is well known. They also resemble Myrtaceae; the presence of Myrtaceae in the Cretaceous period, and also their Australian distribution make affinity with Cactaceae more reasonable if the Cactaceae themselves are primitive. The Cactaceae are specialized, so far as vegetative characters are concerned. Many characters connect Cactaceae with *Mesembryanthemum* and with Portulacaceae (Chorinsky, 1); these suggest changes from parietal to axile and to central placentation. Though Engler accepted the affinity of Cactaceae to *Mesembryanthemum*, this idea was not carried into his system.

Tamaricaceae and Frankeniaceae are families with basal or parietal placentation. *Frankenia*, in numerous characters so near *Dianthus*, has in different species parietal and basal placentation. Frankeniaceae and Caryophylaceae were placed together in the Bentham-Hooker and older systems. Together they make a reasonable connection to families with central placentation (6). The position of these families in the Engler system is especially unsatisfactory.

It does not seem desirable to use the terms pistil or placentation in



Figs. 4–7. Placentation in flower buds and in flowers.

speaking of plants like *Magnolia*, *Ranunculus*, *Rosa* or *Berberis*, with carpels separate or single. For these plants the term carpel is preferable, thus limiting the word pistil to flowers with fused carpels. Placentation we consider to relate to the structure of fused carpels only. Primitive

placentation means placentae fused by two's along the margins of adjacent carpels, that is, placentae in separate groups; but axile placentation means more extended placentae united in the center. Axile placentation is an improvement on parietal placentation in somewhat the same way that epigyny is an improvement on hypogyny, for the growing ovule needs nourishment and protection, and these requirements are better supplied in epigyny and in axile placentation than in hypogyny and in parietal placentation. We have thus for placentae essentially the same development as for petals, sepals, or carpels, namely, from separate to united parts. Carpels from separate to united, placentae from separate to united, and petals from separate to united appear to briefly summarize stages of various phylogenetic lines of floral evolution.

The terms ovary and placenta have been taken over from zoology to botany because of similarity of function, the ovary to contain, the placenta to nourish the growing organism, whether animal or plant. In zoology, the coming of placental mammals marks a definite step in evolution, namely increasing care of the next generation. In botany the term ovulary has been proposed. Whatever the name, to assign to placentation a more important place in the classification of the higher plants calls attention to a significant analogy between plant and animal evolution.

SUMMARY

For many characters, such as sympetaly, zygomorphy and epigyny, the ontogeny of flowers confirms accepted views of phylogeny.

But while flowers with parietal placentation are similar in the bud and in the adult form, those with axile placentation usually have a beginning of parietal placentation in the bud.

If groups with parietal placentation, such as Opuntiales, Parietales and Papaverales, are placed together early in the system the classification becomes more natural.

Brooklyn Botanic Garden
February, 1939

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Lagenospermum imparirameum sp. nov., a Seedbearing Fructification from the Mississippian of Pennsylvania and Virginia[1]

CHESTER A. ARNOLD

(WITH TEN FIGURES)

The fructifications described in this account are the first of their kind to be recognized in the Mississippian (Lower Carboniferous) of North America. Previous descriptions of the flora have dealt mainly with vegetative remains. Fructification material has been found recently at several places, but the largest quantity was collected from an outcrop of the Pocono in the railway cut west of the bridge (known as High Bridge) over Fishing Creek about one fourth of a mile west of Outwood, Schuylkill County, Pennsylvania. At this place the plantbearing beds are accessible along the south side of the track in a vertically tilted stratum of dark gray shale which is about one hundred feet thick and flanked on either side by massive sandstone. The best material was secured in 1936 when a large number of seeds were found in a thin zone near the eastern extremity of the exposure. During two later visits to the place only a few were found. A goodly quantity of specimens was also collected from the black shale of the Price formation on the dump of the Merrimac mine near Blacksburg, Virginia, and a few isolated seeds are present among a small collection of Pocono plants from Allegrippus west of the Horseshoe Curve in Blair County, Pennsylvania.

The Pocono and Price formations are of similar age, and constitute the basal members of the Mississippian in the Appalachian region. The distribution of *L. imparirameum* indicates that it may be one of the characteristic species of plant fossils in these formations.

The fructifications are small, terminal, seedbearing husks on bifurcated stalks of slightly unequal length (Figs. 1–8). Their affinities are apparently with the lyginopterid group of the Pteridospermeae and they appear to fall within the confines of *Lagenospermum*, a genus instituted by Nathorst for fructifications which resemble *Lagenostoma* but lack internal structure. They are also referable to Goeppert's form genus *Calathiops* (4), although this seems less desirable for reasons to be discussed. Goeppert's diagnosis of *Calathiops* is brief and the name was proposed

[1] Paper from the Museum of Paleontology and the Department of Botany of the University of Michigan. The material was described before the Paleobotanical Section of the Botanical Society of America at Indianapolis, Indiana, on December 28, 1937, under the title *The Morphology of Calathiops and Its Occurrence in North America*. (Abstract in Amer. Jour. Bot. vol. 24, p. 743. 1937.)

merely for naked, subdichotomously branched axes bearing terminal tufts of basally joined lanceolate-linear bractlets which may sometimes enclose a seed. Goeppert, however, observed no seeds in his material, and the name has subsequently been applied to several indeterminate fructifications answering this brief description. Some of the fructifications which have been placed in *Calathiops* are probably pollenbearing organs. Therefore, since an assignment to *Calathiops* does not imply either a seed or a spore producing organ, a fructification in which the contents are known should preferably be assigned to some other genus. Goeppert's account of *Calathiops* was included in a large work dealing primarily with Permian plants, and consequently the name was long overlooked as a generic cate-

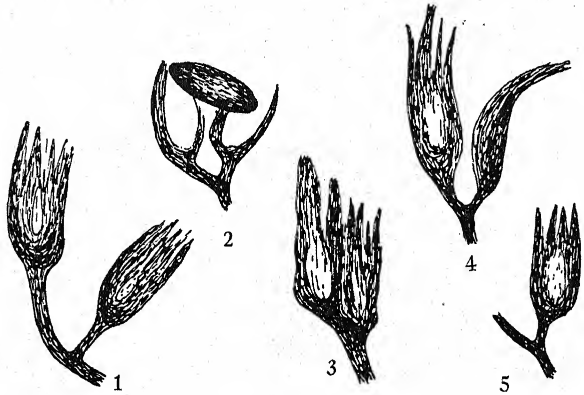

Fig. 1. Seed cupules borne upon pedicels of unequal length, ×about 2.

Fig. 2. Pair of cupules showing a seed only slightly displaced from its original position, ×about $1\frac{1}{2}$.

Fig. 3. Cupule pair borne upon very short unequal pedicels, ×about 2.

Fig. 4. Specimen similar to that shown by Fig. 1, ×about $1\frac{1}{2}$.

Fig. 5. Single well preserved cupule, ×about $1\frac{1}{2}$.

gory for early carboniferous or Devonian fructifications. Otherwise many forms which have received such names as *Schuetzia*, *Alcicornopteris*, *Ptersispermostrobus* or *Xenotheca* might have been referred to it.

The stalks which bear the seed husks of *Lagenospermum imparirameum* branch dichotomously. The terminal cupules are produced either upon slender, leafless stalks resulting from a single bifurcation (Figs. 1, 2, 4, 5, 6, 7) or in pairs upon very short stalks resulting from a secondary forking (Fig. 3). A single primary stalk may therefore bear two, three or four cupules, depending upon the number of ultimate branches. The branches resulting from the first bifurcation are 1 mm. or less in diameter, and range up to 12 mm. in length. If secondary branching occurs, the branches

are always short and the two terminal cupules are borne in such close proximity that they often appear as a single fructification which is somewhat broader than the ordinary ones (Fig. 3). Even in such fructifications, however, the unequal dichotomy is visible because one cupule of the pair is usually slightly lower than the other, giving the false impression of a single body with an oblique base.

The individual cupules are about 3 mm. wide and 9–10 mm. long, and appear to consist of five slender bracts joined basally for about two thirds of their length. Within the cupule the seed is borne. The free ends of the bracts extend beyond the seed as sharp tapering points. It is evident, therefore, that the cupule of *L. imparirameum* is similar to that of the well known *Lagenostoma Lomaxi* (except for the lack of the capitate glands which characterize that species) and the plant which bore it is probably a member of the Lyginopterideae.

The exact manner in which the seeds were attached within the cupules is not apparent although each cupule appears to contain a single one (Fig. 8). The larger specimens which appear as if they might contain more than one seed should be interpreted (as previously explained) as a pair borne in close proximity on very short pedicels. These paired cupules are placed nearly parallel to each other, although they may be produced at slightly different levels.

Detached seeds have been observed among the cupules from High Bridge and the Merrimac Mine, as well as other places. One cupule from High Bridge shows a seed only slightly displaced from its original position (Fig. 2). The seeds are oval, and measure approximately 2 mm. in diameter and 5 mm. in length (Fig. 9). They are enclosed except at the tips by the joined bases of the surrounding bracts. Very little of the tissue of the seed is preserved except an amber colored surface membrane on which a rather characteristic reticulate pattern may be seen (Fig. 10). This pattern is so pronounced that it serves to identify the detached seeds at places where the cupules were not found.

That these oval bodies are seeds rather than spore cases is indicated by the fact that they produce shallow concavities filled with carbonaceous material in the dark shaly matrix. No spores have been found in the several specimens macerated. The form of the seeds is simple without the prominent testal angles or ridges which so frequently characterize Paleozoic seeds, although such features might have been obliterated by the extreme pressure to which these seeds had been subjected.

No foliage has been found attached to *L. imparirameum* although the leaf type recently described as *Cardiopteridium Holdeni* (7) is abundant wherever the seeds or cupules occur. A small slab from High Bridge bears

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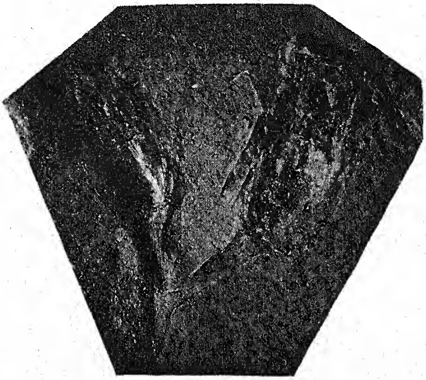

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Fig. 6. Holotype specimen. From the Price formation, Merrimac Mine, Va. *No. 20798*, Univ. Mich. Coll., ×3.

Fig. 7. A specimen similar to that shown in Fig. 6, less well preserved but the position of the seed is shown in each capsule. Paratype. From the Pocono at High Bridge, Pa. Univ. Mich. Coll. *No. 20901*, ×3.

Fig. 8. Single cupule showing the outline of the compressed seed. Other data as for Fig. 7.

Fig. 9. Detached seed, ×about 7. Other data as for Fig. 7.

Fig. 10. Enlarged view of seed surface showing characteristic reticulations, ×20.

a pinnule which was probably attached to a seedbearing stalk, but a break in the matrix destroys the organic continuity if such existed. Several forms of *Triphyllopteris*, *Rhodea*, and *Adiantites* also occur, but not so intimately. The published figures of *C. Holdeni* are indistinct, but material collected at High Bridge and the Merrimac mine reveals its characters adequately.

The associated foliage (*C. Holdeni*) appears identical with that erroneously referred by Lesquereux in the *Coal Flora* (9, Pl. XLIX, Figs. 1–3) to *Archaeopteris Bochschiana* but transferred by Kidston (8, p. 414) to *Aneimites acadica*. The similarity extends to such features as the outlines of the pinnules, venation, mode of branching and especially to the long acutely tapering base of the terminal pinnule. The resemblance to Lesquereux's figures is so close that there can be no doubt about specific identity.

The previously described Paleozoic fructifications with which *L. imparirameum* may be compared are known under a variety of names. Were it not reasonably certain that the fructification bears seeds, *Calathiops* would be the appropriate name for it. However, a seed is definitely present, and as far as external appearances are of value in expressing affinities, the resemblance is certainly closer to *Lagenostoma* than to any other structurally preserved seed type.

Lagenospermum Sinclairi, described by Arber (1) from the Lower Coal Measures of Ayrshire, resembles *L. imparirameum* in the possession of a cupulate seed borne terminally on a naked forked pedicel. There is also some similarity in size and Arber states that the cupule of this form is 3 mm. broad by about 8 to 9.5 mm. in length. The seeds of the two forms are similar although no reference is made to surface configuration on *L. Sinclairi*. A slight difference may be noted in the length of the apical lobes of the cupules. Those of *L. Sinclairi* are said to be from 1.5 to 2.5 mm. whereas those of *L. imparirameum* may project for 3 or 4 mm. beyond the apex of the seed. The branching of *L. Sinclairi* is not so strictly dichotomous. Aside from these and other minor differences the two forms appear essentially alike.

Pterispermostrobus bifurcatus (Stopes, 10) from St. Johns, New Brunswick, resembles *L. imparirameum*, but in the absence of seeds this form must be retained within the *Calathiops* category. The campanulate seed cups of both forms consist of joined bracts which are free at the tips, but in *P. bifurcatus* the seedbearing pedicels are of equal length, and the bifurcated branches are spaced at intervals of about 1 centimeter along the main rachis. Also, as may be noted when measurements are compared, the cupules of *L. imparirameum* are slightly larger. Apparently the two

forms are the seedbearing organs of similar plants, although sufficient differences exist to denote specific separation.

Benson (3) and Gothan (6) have described a seedbearing structure under the name of *Calathiops Bernhardti*. This fructification differs from *L. imparirameum* in several important respects, and it probably belongs to a different group of pteridosperms. The cupules of *C. Bernhardti* are larger and the seeds are rounded bodies, and it differs further in that the cupules appear to be crowded into dense clusters on sympodially produced stalks. Gothan (5, Pl. I) also figures a specimen of *Calathiops plauensis* which closely resembles *L. imparirameum* after the seeds have become detached from the cupules. Although none of the cupules of *C. plauensis* reveal seeds, one cupule in particular shows an empty central area flanked on either side by fibrous bracts. The entire organ resembles a seed receptacle and the central space occupies the same position as does the seed of *L. imparirameum*. It therefore seems probable that *C. plauensis* is a seedbearing organ of the *Lagenospermum* type.

Paired objects resembling cupulate seed husks occur in the Upper Devonian of Pennsylvania (2). Although these organs bear a close resemblance to the Pocono fructifications, the presence of seeds in them has not been demonstrated. However, they more closely resemble seed husks than any other structures known from the Devonian.

Numerous references to *Calathiops*, *Telangium Calymmatotheca*, *Alcicornopteris* and *Schuetzia* may be found in the literature on early Carboniferous plants. For the most part these fructifications consist of terminal acicular bracts on dichotomously forked axes, and some are supposed to represent microsporangiate organs. It is interesting to note that among fructifications of this type the pollenbearing and the seedbearing structures are sometimes difficult to distinguish, and this similarity may have some bearing on the problem of the origin and evolution of the seed. It may be postulated that from the single, terminal sporangium of the psilophytalean type of the early Devonian, there developed during the later Devonian and the early Carboniferous, the *Calathiops* type of fructification. Some members of these bore microspores but others bore megaspores. By the retention and enlargement of the megaspore, the rather simple, terminal, cupulate seed of the *Legenospermum* type developed. *Telangium*, probably belonging to *Lyginopteris*, may be interpreted as the more completely differentiated microsporangiate organ which still resembles the primitive undifferentiated type of fructification by being borne terminally on leafless, bifurcated branches. These terminal, and bracteate or cupulate organs may therefore represent certain stages in the evolutionary development of the pollen producing and the seed producing organs. The terminal

position of these fructifications on bifurcated and leafless axes is comparable to that of the most primitive vascular plants known, the Psilophytales, and support is thereby lent to the recent hypothesis based upon paleobotanical evidence that the seed might have been a terminal organ at the time of its origin, and that it evolved independently of the leaf.

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Notes on the Botanical Components of Curare—II

B. A. Krukoff and A. C. Smith

The first paper in this series, discussing the botanical components of Curare as prepared by the Tecuna and Java Indians of Brazilian Amazonia, was published in 1937 (5). Dr. K. Folkers (1) has published preliminary chemical and pharmacological studies of the material obtained from the plants which were the basis of our botanical work. Now, through the courtesy of Mr. Richard C. Gill, we are able to examine specimens of the plant components of the Curare of the Canelos Indians of Ecuador. Specimens discussed in the present paper were collected by Mr. Gill on the Gill-Merrill Ecuadorian Expedition in August to October, 1938, having been obtained in the Pacayacu–Sarayacu region, drained by tributaries of Rio Pastaza in the Province of Napo-Pastaza. The collection is of unusual interest, since there appears to be no published record of the botanical identity of a single plant which the various Indian tribes of Ecuador use in preparing Curare. This is true in spite of the fact that many of these tribes, such as the Canelos, Jibaros, and others, are known to use blow-guns and Curare extensively and have been visited on many occasions by various explorers.

The crude material of plants used by the Canelos Indians in the preparation of the poison is now under chemical and pharmacological study in the Research Laboratory of Merck & Co., Inc., and at the Merck Institute of Therapeutic Research, Rahway, New Jersey. Botanical specimens mentioned in this paper are deposited in the herbarium of the New York Botanical Garden, unless otherwise noted. We take this opportunity to thank Prof. S. J. Record and Dr. R. A. Cockrell for their cooperation in checking our determinations of certain sterile plants on the basis of wood samples.

CURARE OF THE CANELOS

During his stay in the territory inhabited by the Canelos Indians, Mr. Gill had the opportunity to observe the preparation of Curare in several localities and by different poison-makers. He has kindly made available to us extensive notes regarding these preparations. Below we shall list the quantities, parts of the plants, and botanical names of the plant components of Curare as Mr. Gill saw it prepared in different localities. From these, as well as from several other "recipes" obtained by Mr. Gill but not given here because of space limitations, it is evident that the Canelos as a rule use the same main ingredients. The quantities and the secondary ingredients vary considerably from locality to locality and with different

poison-makers. These facts are also true, in a general way, of other South American tribes which prepare Curare.

We do not consider it worth while to discuss here the details of Curare preparation by the Canelos, since this subject has been covered by Karsten (3: 149–152) and others. However, we shall briefly call attention to the more important features of the preparation as observed by Mr. Gill. The ingredients, regardless of what portion of them is used, are thoroughly macerated and mixed together in large earthenware containers with an adequate amount of water. Thereafter the whole process consists of boiling until the Curare approaches its final stage and becomes thick and syrup-like. During this boiling, the mixture has been strained two or three times and the surface scum has occasionally been removed. The Curare is finally brought to the desired concentration in a small container over a very slow fire to guard against scorching.

The important feature of Curare preparation by the Canelos is that they use the macerated whole stems of their main menispermaceous ingredients rather than merely the bark. In addition, they boil the ingredients rather than carry out the extraction of the active principles with cold water. In these respects the method of preparation is similar to that of the Chazutas of Peru and notably different from that of the Tecunas and Javas of Brazil.

Approximate quantities of various ingredients used in the preparation of Curare by the Canelos Indians.

1. AS PREPARED IN THE VICINITY OF PACAYACU:

Stems of *Chondodendron iquitanum* ("Tonispa Pala Ango")	17.5 pounds
Stems of *Chondodendron tomentosum*	11 pounds
Stems of *Chondodendron iquitanum* ("Nana Tonispa")	11 pounds
Bark of stems of *Strychnos Mitscherlichii*	1.5 pounds
Bark of *Ficus* sp.	1 pound
Bark of roots of *Annona Ambotay*	1 pound
Two small whole roots of *Lonchocarpus utilis*	8 ounces

2. AS PREPARED BY A SECOND POISON-MAKER IN THE VICINITY OF PACAYACU:

Stems of *Sciadotenia toxifera*
Stems of *Chondodendron iquitanum* ("Tonispa Pala Ango")
Bark of roots of *Annona Ambotay*
Two small whole roots of *Lonchocarpus utilis*
Stems of *Chondodendron tomentosum*

3. AS PREPARED BY A THIRD POISON-MAKER IN THE VICINITY OF PACAYACU:

Stems of *Chondodendron iquitanum* ("Tonispa Pala Ango")	12 pounds
Stems of *Sciadotenia toxifera*	11.5 pounds
Stems of *Chondodendron tomentosum*	26 pounds
Bark of roots of *Strychnos Jobertiana*	1 pound
Whole root of *Erythrochiton* sp.	1 pound
Bark of roots of *Strychnos* sp. (*Gill 9*)	1.5 pounds
Bark of roots of *Strychnos Peckii*	12 ounces

Whole root of *Gill 24*	4 ounces
Bark of *Gill 25*	4 pounds
Bark of *Ficus* sp.	2 pounds

4. AS PREPARED IN THE VICINITY OF RIO CONAMBU:

Stems of *Chondodendron iquitanum* ("Yana Pala Ango")	6.5 pounds
Stems of *Chondodendron iquitanum* ("Tonispa Pala Ango")	11 pounds
Bark of roots of *Sciadotenia toxifera*	4 ounces
Stems of *Cissampelos pareira*	4.5 pounds
Bark of stems of *Strychnos toxifera*	2.5 pounds
Bark of stems of *Strychnos Peckii*	8 ounces
Bark of branches of *Gill 38*	1 pound
Bark of roots of *Strychnos* sp. (*Gill 9*)	2 ounces

SPECIMENS EXAMINED FROM THE TERRITORY INHABITED BY THE CANELOS INDIANS

MORACEAE

FICUS sp. The collection *Gill 7* suggests *F. paraensis* Miq. by the general shape and texture of its leaves, but has shorter petioles and lacks the prominent veinlet reticulation of the upper leaf surface which characterizes Miquel's species. *F. atrox* Mart. was reported (Buchner, Repert. Pharmacie **36**: 341. 1830; Lond. Jour. Bot. **6**: 550. 1847) as used in Curare, but that species has ovate leaves deeply cordate at the base and apparently is not closely related to ours. According to Gill, the present species is known to the Canelos as "Yana Ambi Caspi." Its bark is occasionally used as a secondary ingredient of Curare. It is probably the same species to which Karsten (3: 148) refers as "Yána hámbi cáspi."

MENISPERMACEAE

CHONDODENDRON IQUITANUM Diels. Of the plant components of Curare as prepared in different localities by the Canelos poison-makers, this species appears to be most commonly used as a main ingredient. All the preparations of the Canelos recorded by Gill include this plant, and in most cases it is used in quantities exceeding those of other ingredients. The macerated entire stems, including bark, are usually used. According to Gill, many poison-makers claim that this species alone makes a potent poison; he also states that it is common throughout the region.

We place in this species *Gill 6*, *12*, and *35*, collected under the names of "Nana Tonispa," "Tonispa Pala Ango," and "Yana Pala Ango" respectively. It appears from the collector's notes that the Canelos distinguish the three plants; although the specimens are sterile we place them in this species with confidence. These collections are the first record of the species from Ecuador, it being otherwise known only from the type locality in Peru near the mouth of Rio Santiago, above Pongo de Manseriche. The

species has recently been reported (4: 25) as used in Curare by certain Peruvian Indians. Karsten (3: 147), in listing the Quichua names of the plants used in Curare by the Canelos Indians, mentions "Pála huásca" as "a big flat liana, about 12 to 15 cm. in breadth. . . . Because of its flatness it is called 'the shovel-liana' (*pala* = 'shovel')." This seems to explain why two of the common names recorded by Gill for *C. iquitanum* (which, as all known species of *Chondodendron*, has a distinctly flat stem) make use of the word "pala." The word "tuníshpa," according to Karsten, means "mixed" and is used to suggest the resemblance of one plant to another.

CHONDODENDRON TOMENTOSUM R. & P. The species has recently been reported (4: 18) as the main ingredient of the Curare of the Chazuta Indians of Peru. The present collection (*Gill 20*) is the first record of the species from Ecuador, although it has already been collected in Panama, Colombia, Peru, and Bolivia. The species is an important ingredient of the Curare of the Canelos, second only to *Chondodendron iquitanum*. It is evident from Gill's notes that certain poison-makers use even larger quantities of this plant than of *C. iquitanum*. The poison is made without it only in certain localities in the basin of Rio Conambu. The plant is known to the Canelos as "Tulumba Lamas Ango"; the entire stem, including bark and wood, is usually used by them.

Sciadotenia toxifera Krukoff & Smith, sp. nov. Frutex scandens; ramulis gracilibus teretibus cinereo-fuscis juventute minutissime pilosulis demum glabris; petiolis gracilibus striatis 3.5–6 cm. longis ut ramulis decidue cinereo-pilosulis; laminis maturitate subcoriaceis utrinque fusco-olivaceis late ovatis vel ovato-ellipticis, 14–22 cm. longis, 9–13 cm. latis, basi obtusis vel acutis vel cuneatis, apice abrupte cuspidatis vel caudato-acuminatis (acumine 5–25 mm. longo), margine leviter revolutis et saepe undulatis, utrinque glabris (vel juventute subtus ad nervos principales et secundarios parce puberulis mox glabris), 5 (vel obscure 7)-pli-nerviis, nervis primariis (superioribus 3–15 mm. supra basin orientibus) utrinque prominentibus, costa in laminae apicem terminante, nervis secundariis numerosis horizontalibus utrinque prominulis, venulis minute et conspicue reticulatis utrinque prominulis; inflorescentiis desideratis.

Type, *Gill 11*, collected Aug. 29, 1938, in dense forest near Pacayacu, in drainage of Rio Bobonaza and adjacent tributaries, basin of Rio Pastaza, Province of Napo-Pastaza, Ecuador, alt. 1000 m. *Gill 36*, from the Rio Conambu in the same general region, alt. 900 m., also represents the species.

These two specimens provide the first authentic evidence of the use of a member of this genus in Curare. From *S. similis* Moldenke, *S. Sprucei*

Diels, and *S. cayennensis* Benth., the new species is immediately distinguished by the comparatively large leaves, by the dense and fine veinlet reticulation which is conspicuously prominulous and discernible to the naked eye on both surfaces, and by the fact that the inner pair of principal nerves arises at a distance of 3–15 mm. above the base of the leaf blade. Its leaves are often faintly 7-pli-nerved as in *S. solimoesana* Moldenke, from which it is distinguished by the blades being cuneate to obtuse rather than truncate to subcordate at base, by the veinlets being conspicuously prominulous above rather than subimpressed, and by the fact that the blades are sparsely puberulent on the princpal nerves and secondaries beneath when young and at length glabrescent or glabrous, not obscurely but regularly appressed-puberulent on the lower surface. Although neither inflorescences nor fruits are available, we have no doubt that this is a new species, and it seems preferable to assign a name to it rather than to await more complete future collections.

The species appears to be a consistent and important component of the Curare of the Canelos. It is evident from Gill's notes that the poison is seldom prepared without it, and some poison-makers claim that a good Curare may be made from this plant alone. The entire stems, including bark and wood, are used by the Canelos. In the locality of Pacayacu it has been collected by Gill under the name of "Cuilin Ango," while in the basin of Rio Conambu he obtained it under the name of "Yana Ilucha." It is probably the same species to which Karsten (3: 147) refers as "Cüílin huásca" ("cüílin" = a bird of the toucan family), a small liana about 3 to 4 cm. in diameter.

CISSAMPELOS PAREIRA L. *Gill 20a* seems to agree well with the variety *typica* Diels. According to the collector, in certain localities in the basin of Rio Conambu the plant is used in place of *Chondodendron tomentosum* in Curare and is known to the natives under the same name, "Tulumba Lamas Ango."

A. C. Smith 3229, *Cissampelos ovalifolia* DC., was recently collected on savanna between the Takutu River and the Kanuku Mountains, British Guiana. The actual manufacture of Curare by the Macusi Indians stopped many years ago, but only within the last five years there was still living a medicine man who showed the principal plants which he used in "Urari" to Father H. C. Mather, S. J., of St. Ignatius Mission on the Takutu River. The present species was considered an important component. Possibly it is one of the unidentified plant-components of Macusi Curare listed by Richard Schomburgk (6: 353) under common names.

Annonaceae

Annona Ambotay Aubl. sens. lat. This species has already been reported as a component of the Curare of the Tecunas of Brazil (5: 405) and of the Chazuta Indians of Peru (4: 18). It is represented by *Gill 18;* the common name is reported as "Paguaga" or "Paguaga Caspi." The bark of roots is frequently used by the Canelos as a secondary ingredient of Curare. It is probably the same species as that referred to by Karsten (3: 148) as "Hambi pahuága."

Genus uncertain. *Gill 15* is from a plant known to the Canelos as "Cara Caspi"; its bark is occasionally used as a secondary ingredient of Curare. This is possibly the same species to which Karsten (3: 148) refers as "Hámbi cára cáspi."

Leguminoseae

Lonchocarpus utilis A. C. Smith. This well-known fish-poison, represented by *Gill 53,* has already been reported as a component of the Curare of the Canelos by Karsten (3: 146), who refers to it as "Varváscu." Both Karsten and Gill report that the roots are used for this purpose.

Rutaceae

Erythrochiton sp. *Gill 21* is in fruit, and may be either *E. delitescens* Morton or *E. macropodum* Krause, or possibly an undescribed species. According to Gill the plant is known to the Canelos as "Soliman Caspi," and is occasionally used as a secondary ingredient in preparing the poison. A previous record of the use of Rutaceae in Curare is that of Richard Schomburgk (6: 353). He states that the Macusis use for this purpose the strongly bitter wood of "Manuca," "a tree of the family Xanthoxyleae."

Loganiaceae

Strychnos toxifera Rob. Schomb.; Benth. This species is well-known as the main ingredient of the Curare of the Macusi Indians of British Guiana, as was first ascertained by Robert Schomburgk in 1835 and verified by Richard Schomburgk in 1842. Spruce collected a specimen of it in the Cassiquiare region of Venezuela and reported on the label: "one of the species used by the Cunipusana Indians in the fabrication of Curare." Occasionally it is used in the Curare of the Tecunas of Brazil (5: 402, 406).

The present collection (*Gill 37*) is the first record of the species from Ecuador, extending its range approximately 600 miles to the west. The species thus is now known to occur from the Panama Canal Zone (*Standley*

27542, 28386, 31311, 41042; Pittier 2666; Kenoyer 479, 624; all deposited in the U. S. National Herbarium) to the mouth of Rio Embira (tributary of Rio Tarauaca) in the State of Amazonas, Brazil (*Krukoff 5081*), and from the Northwest District in British Guiana (*La Cruz 1358*) to the Pacayacu–Sarayacu region of the Province Napo-Pastaza in Ecuador. According to Gill the plant is known as "Julin Huasca" or "Julin Huasca Ango"; the bark of its stems is frequently used as a Curare ingredient by the Canelos.

STRYCHNOS GUIANENSIS (Aubl.) Baill. This species has a very extensive range, being fairly common in certain localities; it exhibits extraordinary variation in pubescence, leaf size and form, etc., often even on a single plant, and in addition it probably consists of a number of forms. When the American species of *Strychnos* are revised, many names will doubtless be reduced to synonymy under this binomial. It is not our present purpose to review the concept of this variable species, but we wish to mention certain authentic records of the use of *S. guianensis* and the related species (some of which may be conspecific with it) in Curare.

Schreber (7) reported the species, under the name *Toxicaria americana* Schreber, as one of the components of the Curare of certain tribes of Indians in Surinam.

Humboldt and Bonpland (2) mentioned "Curare" or "Bejuco de Mavacure" as one of the ingredients of the poison as prepared by Indians at Esmeralda on the upper Orinoco in Venezuela. This plant was formally described in 1825 and is the basis of *Strychnos Curare* (H. B. K.) Benth. (Jour. Linn. Soc. **1**: 108. 1856).

The type of *Strychnos depauperata* Baill. (Adansonia **12**: 372. 1879) is from the vicinity of Tonantins, Amazonas, Brazil; it was collected by Jobert and reported by him as one of the two species of *Strychnos* used by the "Kawichanes" Indians in preparing the poison.

The type of *Strychnos Crevauxiana* Baill. (Adansonia **12**: 377. 1879) is from the upper Paru, one of the northern tributaries of the Amazon; it was collected by Crevaux and reported by him as the main ingredient of the Curare of the Trios.

A. C. Smith 2836, a form of *Strychnos guianensis*, was recently collected in the basin of Shodikar Creek (Essequibo tributary) in British Guiana. The plant appears to be the most important component of Wai-wai Balauitú (arrow-poison). It is noteworthy that the Wai-wais, like the Trios, use chiefly the outer bark of roots.

The present collection of *S. guianensis* (*Gill 29*) is the first record from Ecuador, the species being well represented in herbaria from the Guianas, Venezuela, Brazil, and Peru. Doubtless it will also be found in Amazonian

Colombia. According to Gill the plant is usually referred to as "Payanche Chico"; its bark is occasionally used as one of the ingredients of Curare by the Canelos.

STRYCHNOS JOBERTIANA Baill. The type is from the vicinity of Tonantins, Amazonas, Brazil, collected by Jobert and reported by him as one of the two species of *Strychnos* used by the "Kawichanes" Indians in preparing the poison. It is also a component of the Curare of the Javas of Brazil and Peru (5: 407, 409). The plant was re-collected in 1936–37 in the Municipality of São Paulo de Olivença, Amazonas, Brazil (*Krukoff 7786, 7802*). The following specimens, all from the State of Amazonas, Brazil, probably represent a juvenile form of the species: *Krukoff 7990* from the immediate vicinity of Manaos, *Krukoff 7799* from the type locality, and *Krukoff 8848* from the basin of Creek Belem.

The present collections (*Gill 19, 74*) are the first record of the species for Ecuador, extending its range approximately 600 miles to the west. The species, which is obviously related to *Strychnos trichostyla* Ducke, doubtless occurs in Amazonian Colombia and Peru. According to Gill the plant is known as "Quilio Huasca"; its bark is used occasionally as one of the ingredients of Curare by the Canelos.

STRYCHNOS PECKII Rob. The present collection (*Gill 22*) appears to be the first authentic evidence of the use of the species in Curare. *Krukoff 7549, 7581, 7628–7632* inclusive, cited as *Strychnos* sp. in our earlier paper (5: 406) and reported as occasionally used in Curare by the Tecunas in Brazil, represent a closely allied plant which may prove conspecific with *Strychnos Peckii.* These specimens were studied by Sandwith and Krukoff in 1937 and were distributed as "*Strychnos* cf. *Peckii* Rob. var.? (group #1; material inadequate)."

The type of the species is from British Honduras. In South America it has been collected by Ducke in the State of Para, and is represented from the State of Amazonas, Brazil, by *Krukoff 8022* from the immediate vicinity of Manaos, and by *Krukoff 7778, 7780, 7789, 7832, 8973, 9054,* and *9108* from various localities in the Municipality São Paulo de Olivença. The present collection (*Gill 22*) is the first record of the species from Ecuador, extending its range approximately 600 miles to the west. The species obviously has a wide range and is to be expected in the countries between the known extremes.

According to Gill the plant is known as "Canon Huasca"; its bark is occasionally used as one of the ingredients of Curare by the Canelos. It is possible that the same Indian name was recorded by Karsten (3: 147) as "Cáñu huásca." However, he refers to a deep channel running along the

middle of the liana, from which it takes its name ("cáñu" = channel). This description hardly applies to *S. Peckii*.

STRYCHNOS MITSCHERLICHII Rich. Schomb. *Gill 5* appears to be the first authentic evidence of the use of this species in Curare. The plant is not used for that purpose by the Tecunas, although it is by far the most common species of *Strychnos* in their territory.

For a long time the species was considered as probably endemic to British Guiana. Recently it has been found in Surinam and in Brazil. Krukoff's collections from the State of Amazonas were identified by Sandwith and Krukoff and distributed as the following: *S. Mitscherlichii*, *S. Mitscherlichii* var. *pubescentior* Sandwith, *S. Mitscherlichii* var.? (group #18; material inadequate), *S. Mitscherlichii* var.? (group #41; material inadequate), and *S. Mitscherlichii* var.? (group #42; material inadequate). The collections are too numerous to cite here. The species appears to be as variable as *S. guianensis*.

The present collection (*Gill 5*) is the first record of the species from Ecuador. According to the collector it is known as "Caronsi Chaqui"; its bark is occasionally used as one of the ingredients of Curare by the Canelos.

STRYCHNOS sp. *Gill 9* is a sterile specimen in poor condition. We cannot match it satisfactorily with any species known to us, nor can we suggest its affinity. According to Gill the plant is known as "Payanche," and the bark of its roots is occasionally used as one of the ingredients of Curare by the Canelos. This is possibly the same species to which Karsten (3: 147) refers as "Payángshi."

RUBIACEAE

PSYCHOTRIA sp. *Gill 65* cannot be determined with certainty; it is probably an ally of *P. cuspidata* Bredem. The collector reports the common name, among the Canelos, as "Chirapa Caspi"; it is occasionally used as a secondary ingredient of their Curare.

FAMILY UNCERTAIN

Several specimens collected by Gill from species used in Curare by the Canelos are too incomplete to permit family identification. These are listed in the hope that eventually their identity will be determined.

Gill 24 is from a plant which the Canelos call "Seco Ango Callo" and which they sometimes use as a secondary ingredient of Curare.

Gill 25 represents a plant known to the Canelos as "Huayna Toa"; its bark is occasionally used as a secondary ingredient of their Curare.

Gill 38 is from a plant known to the Canelos as "Naucari Caspi"; occa-

sionally they use the bark of its stems and branches as a secondary ingredient of Curare.

SUMMARY

As a result of the study of botanical specimens collected by Mr. Gill, supplemented by his notes, we can draw the following conclusions.

1. The principal components of the Curare of the Canelos are invariably members of the Menispermaceae. In this respect their Curare resembles that of the Chazuta Indians of Peru, while it differs notably from the more eastern Curares such as those of the Javas, Tecunas, Trios, and Wai-wais of Brazil, of the Macusis of British Guiana and of certain tribes of the upper Orinoco basin in Venezuela. The main components of these Curares are species of *Strychnos*.

2. *Chondodendron iquitanum* appears to be the main ingredient of most preparations of the Canelos, while *C. tomentosum* and *Sciadotenia toxifera* are usually other important ingredients.

3. One or more species of *Strychnos* are often used in the Curare of the Canelos, *S. toxifera* being the most commonly used. However, it seems evident that the Canelos do not consider species of *Strychnos* to be essential ingredients, as the poison is often prepared without them.

4. A number of plants other than Menispermaceae and *Strychnos*, used as secondary ingredients by the Canelos, are of the same or related species which have already been reported as components of Curare of other South American Indians.

5. The absence of species of *Piper* in the Curare of the Canelos is conspicuous; in this respect it approaches the poison prepared by the Chazutas and differs from that prepared by the Tecunas, Javas, Trios, and Wai-wais.

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The Morphology and Phylogenetic Position of the Genus Jouvea (Gramineae)[1]

PAUL WEATHERWAX

(WITH ELEVEN FIGURES)

On the Pacific coast of Mexico and Central America there are two grasses, constituting the genus *Jouvea,* which present certain unsolved problems of morphology and taxonomy. The two species, *J. straminea* Fourn. and *J. pilosa* (Presl.) Scribn., are apparently concise and at the same time sufficiently distinct from each other to conform with any ordinary concept of the species in general; but the correct position of the genus itself is not so well determined.

The staminate inflorescence is so similar to those of other grasses that it is easily understood. The pistillate inflorescence, however, shows no external resemblance to the staminate, and morphologically it seems to have no counterpart anywhere in the grass family. Different interpretations of it have been given, but no serious morphological study of it has ever been made. It was a statement of the need of such a study, in a comparatively recent taxonomic work (Hitchcock, 1930, p. 585) which first drew my attention to this genus and led me to make a side-trip from Guatemala City down to San José, in March, 1932, to secure specimens and see the plant in the field.

HISTORICAL

The genus *Jouvea*, established by Fournier in 1876, was based upon a pistillate plant of *J. straminea,* which he found in a collection made by Liebmann in Mexico several years previously. There is something of the ironical in Fournier's experience with this species. Having only the pistillate form and apparently misinterpreting that, he gave it a taxonomic position which has been difficult to maintain, and he drew from it a part of a generalization on monoecism and dioecism which the staminate form now completely refutes (Prat, 1933, p. 387). If Fournier had correctly interpreted the Liebmann collection, he might have avoided these errors, for it contained also staminate specimens of *Jouvea* (Scribner, 1896, p. 141).

[1] Contribution No. 77 from the Waterman Institute of Indiana University.

This is one of a series of studies on tropical American grasses, the collection of which was made possible by grants from the American Association for the Advancement of Science, the Society of the Sigma Xi, and the National Research Council and by aid of many kinds given by the United Fruit Company. Support for these studies has also been provided for many years by Indiana University through the Waterman Institute and the research facilities of the Graduate School.

Aside from its inclusion in taxonomic works, without additional information of a critical nature, we next meet *Jouvea* in the literature in 1890, when Vasey and Scribner separately report having found specimens in a collection made by E. Palmer in Lower California.[2] The plant which they describe, with good figures, is evidently what is now known as *J. pilosa*, but this name was not to be applied to it until later.

Vasey (1890) gives a good description of the plant and discusses the significance of the pistillate inflorescence. Not satisfied with Hackel's opinion that it should be placed in Fournier's genus *Jouvea*, he assigns it to a new genus and names the species *Rachidospermum mexicanum*. Vasey's difficulty was partly in the fact that he did not have access to Fournier's original description and partly in his not knowing that he was attempting to reconcile the characteristics of *J. pilosa* with a description of *J. straminea*.

Scribner (1890) more fortunately recognizes the plant as a species of *Jouvea* and tentatively assumes that it is *J. straminea*, although he admits that it does not agree with the description in all details. His figures, which are unmistakably of staminate and pistillate specimens of *J. pilosa*, are labeled "*Jouvea straminea*, Fourn.?".

In a second article (1896), Scribner corrects his error in identification and recognizes the two species, *J. pilosa* and *J. straminea*, essentially as we know them to-day.

The morphological findings of these investigators will be discussed in connection with the description and interpretation of the pistillate inflorescence.

MATERIAL

Jouvea pilosa proved to be an easy plant to find at San José; it formed almost a continuous colony along the top and seaward slope of the ridge of black sand on the two miles or more of beach examined. At first, *J. straminea* seemed not to be present, but, thanks to a few prominent staminate plants, it soon became evident that literally acres of the marshy flats on the landward side of the beach ridge were covered with it. The dull, bluish-green color and wiry habit of the plants had caused me to relegate them temporarily to some other family, such as the Juncaceae.

Aware of the species problem involved when two closely related plants occur together in this way, I spent some time looking for indications of hybridization but found none. In many places male plants of one species

[2] Note that this is Lower California, not California. As far as is known at present, *Jouvea* has not been found within the United States. Prat's statement (1933, p. 357) that it is found in California is probably due to the assumption that Lower California is a part of California.

were certainly close enough to females of the other for cross-pollination to occur; and the fully exposed stigmas, typical development of the anthers, and dioecious nature of both species indicate that wind pollination most certainly occurs.

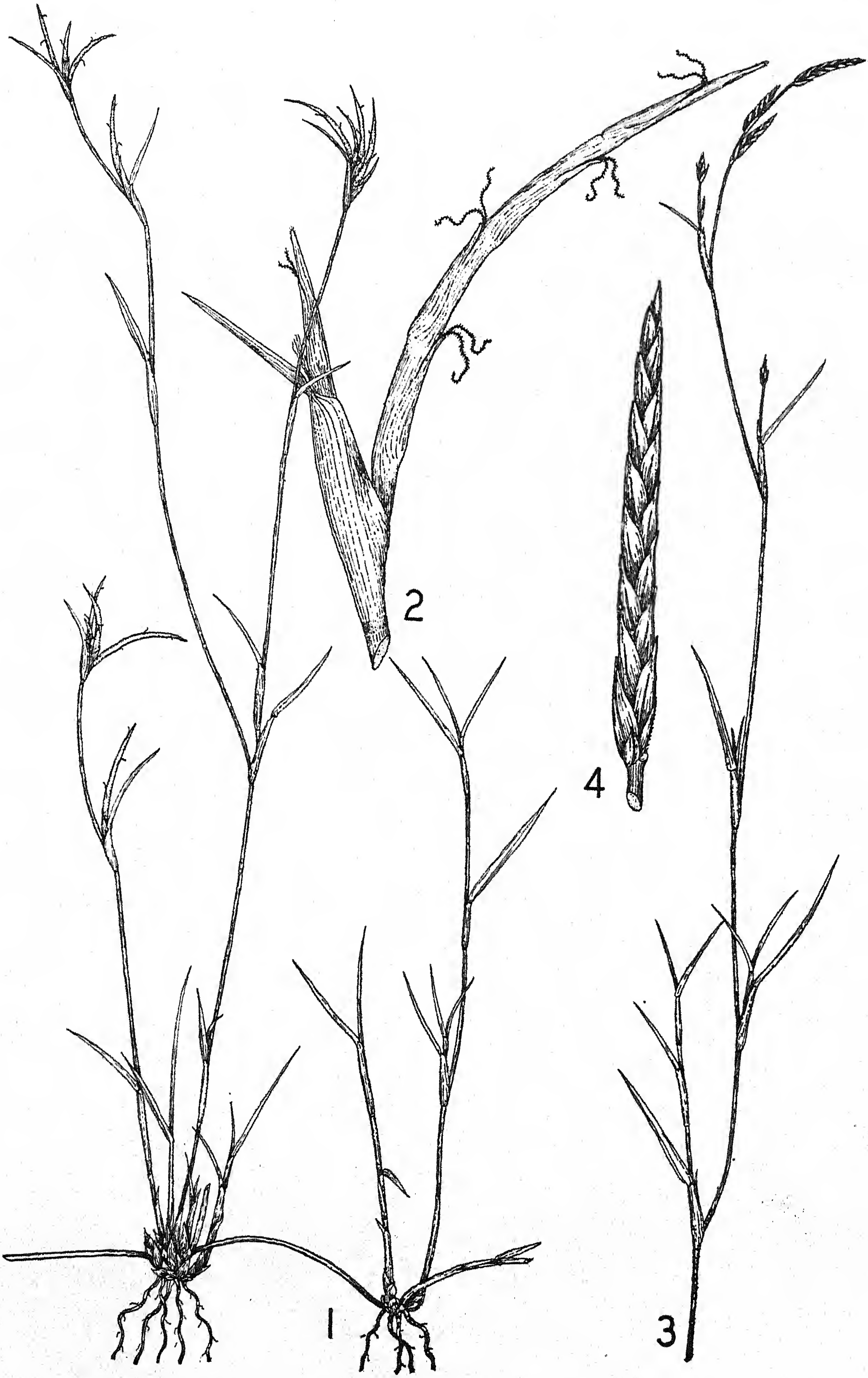
From the material collected it has been possible to make a very satisfactory study of most of the morphological features which seem to have any bearing on the phylogeny of the genus and the homologies of the pistillate inflorescence. Sufficient herbarium material has been available that an almost unlimited amount could be dissected and the range of variation of different parts studied. From collections preserved in formal-acetic-alcohol, good microtome sections have been made of stems, leaves, spikelets, and even entire fascicles of young pistillate inflorescences. Seeds of *J. pilosa* have also been germinated so that the structure of the seedling could be studied, but greenhouse conditions were apparently not favorable for the growth of seedling plants to maturity.

STAMINATE INFLORESCENCE

If all parts of these plants were as amenable to interpretation as are the staminate spikelets, the problem would be simple. As far as they alone are concerned, the resemblance to *Uniola*, *Distichlis*, *Lolium*, or *Agropyron* would suggest affinities with the Festuceae or the Hordeae, the final allocation depending upon characteristics outside the spikelet.

In *J. pilosa* (Fig. 6) some of the staminate spikelets are short and oblong, containing from 10 to 15 florets, while others are longer, linear in shape, and containing from 25 to 50 florets. These two types, although fairly distinct, seem to be due to environmental factors. At the time of year at which the collection was made (March) all of the long spikelets were old and weather-beaten, while the short ones were still alive, some even immature, but complete as to primordial development. The corresponding spikelets of *J. straminea* (Figs. 3, 4) are essentially like those of *J. pilosa* but smaller. They usually have from five to seven florets and seldom more than 15 or 20.

In both species the staminate spikelets are arranged in long-peduncled, definitely dorsiventral spikes, with the uppermost spikelet apparently terminal on the rachis. In *J. pilosa* the spikes are clustered in axillary fascicles, each of which consists of a short branching system, leafless except for prophylls, with the end of each ultimate branch elongating to form the spike. In *J. straminea* these axillary branches are more simple, each usually producing one, and seldom more than two or three spikes. The spikelets are acropetal in flowering, but any one inflorescence produced from an axillary branch is basipetal.

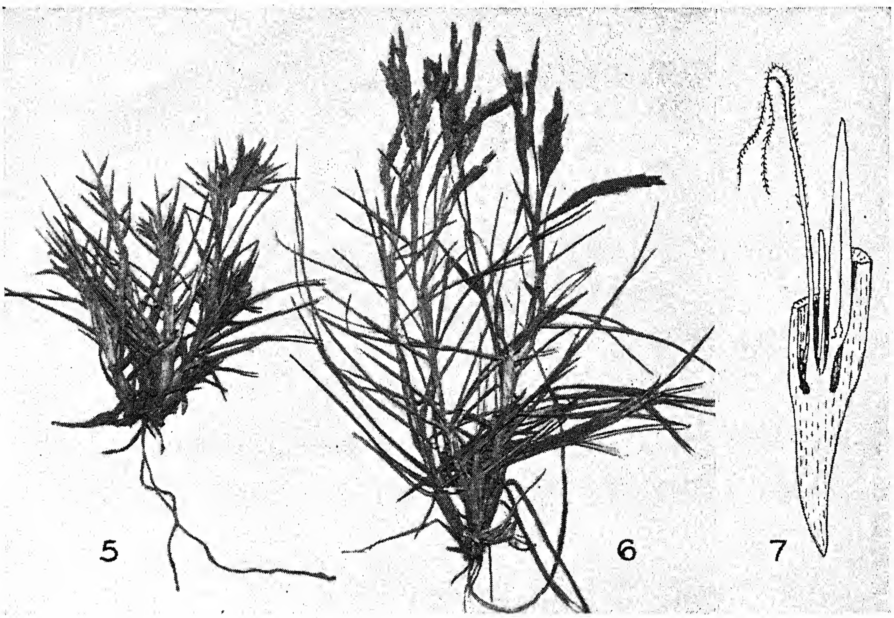


Figs. 1–4. *Jouvea straminea.* Figs. 1, 2. Pistillate plant and spikelet. Figs. 3, 4. Staminate plant and spikelet.

The staminate florets have the usual lemma and palea and a flower consisting of two lodicules and three stamens. There is no visible rudiment of a pistil and apparently not even a vascular rudiment leading to the position where a pistil would be expected.

PISTILLATE INFLORESCENCE

The ultimate unit of the pistillate inflorescence is a curved, thorn-like structure, in the sides of which the flowers are imbedded in two rows in alternate arrangement (Figs. 2, 10). In *J. pilosa* (Fig. 10) the number of



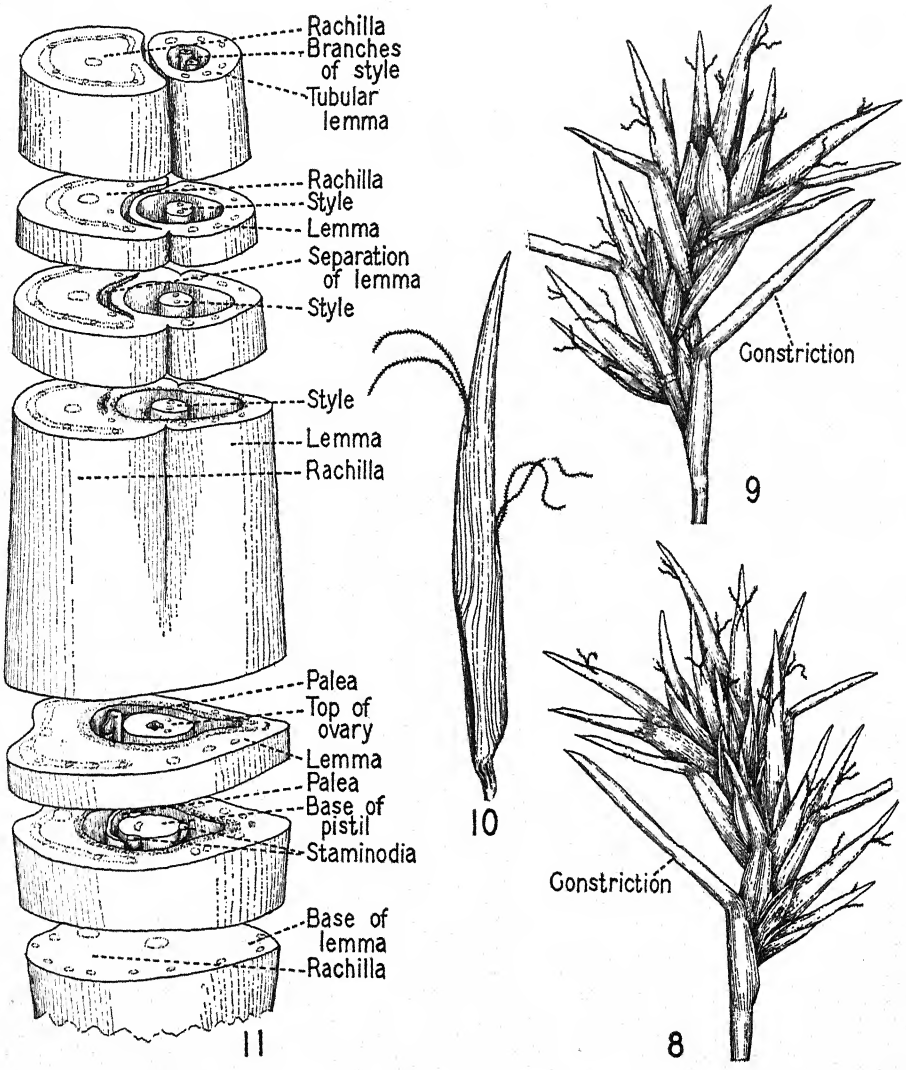
Figs. 5, 6. Pistillate and staminate plants of *Jouvea pilosa*. Fig. 7. Copy of Scribner's figure, showing a second flower (*J. straminea*).

flowers may be as low as two, with sometimes only the lower one functional; but in *J. straminea* (Fig. 2) there may be as many as four or five, with only the uppermost one rudimentary.

The morphological interpretation of this pistillate structure is the problem. Does it consist of a rachis with greatly reduced one-flowered spikelets imbedded in it, so that it resembles the *spike* of *Lepturus*, *Rottboellia*, *Tripsacum*, or *Stenotaphrum*, or is it an anomalous *spikelet* with the flowers imbedded in the thickened rachilla? Both views have been held, but no thorough morphological analysis has ever been made.

Fournier (1876, pp. 475–476) seems to have no other idea than that this structure is a spike, with the one-flowered spikelets imbedded in the

rachis. He describes the spikelets as having two glumes, with the inner separate from the rachis only at the top, and two small, narrow palets.[3]



Figs. 8–11. *Jouvea pilosa.* Figs. 8, 9. Ventral and dorsal views of a pistillate branch. Fig. 10. Pistillate spikelet. Fig. 11. Diagrammatic view, drawn to scale, of a pistillate spikelet sectioned at seven levels through one floret.

Vasey (1890) also raises the question of the morphology of the pistillate part of the plant. Without citing any real evidence, he agrees with

[3] "Glumae 2, exterior cartilaginea, straminea, interna hyalina, apice tantum a rachide distincta. Paleae duae, angustae, minores."

Fournier that it is a spike with the spikelets imbedded in the thickened rachis, each of the latter being reduced to a single pistil and possibly a lemma.

Scribner's interpretation (1890) of it as a spike agrees in most repects with the preceding, although he correctly points out that Fournier's description mentions some parts which cannot actually be found in the material. In a second article (1896) he gives, for the first time, serious consideration to the idea that the pistillate structure may be a spikelet, with the florets imbedded in a thickened rachilla, and that its resemblance to the spikes of *Lepturus* and *Monerma* may be only a simulation. But he makes one other interesting observation. In describing the pistillate "spikelet" he says (p. 143) that in many instances in *J. straminea* he found, above the palea of the ordinary floret, a second, imperfectly developed pistil enclosed in a membranous sac like that around the perfectly developed flower (Fig. 7). This would constitute almost positive evidence that the imbedded structures were spikelets rather than florets; and it is difficult to see why, in possession of a unique bit of evidence favoring one side of the question, he should conclude with exactly the opposite view. He clearly recognizes the significance of the point but apparently chooses to ignore it.

Hitchcock at one time (1913, pp. 190, 384) regards the structure as a spike; later (1930, p. 585) he calls it a spikelet but adds: "However, that which is called a spikelet may be a spike with 1 to 3 spikelets imbedded. Morphological research is needed here."

All evidences which I have been able to obtain from the material at hand lend support to the view that the pistillate structure in question is a spikelet, and future references to it, including the labels of the figures, will be made from this point of view. This does not entirely eliminate the possibility of some future observation which might change the picture. The evidence is mostly negative in nature. To call it a spike is to imply more deviation from the type of its staminate homologue than is necessary in view of what we know about it.

In some ten or twelve flowers of each species from which good series of sections have been obtained, there is perfect uniformity in all details which are regarded as significant; and these results have been substantiated by the dissection of probably 200 florets of each of the species from herbarium material.

The spikelet consists of a thick, spongy rachilla with the flowers deeply imbedded in its sides (Figs. 2, 10). The lowest flower of the spikelet seems to be, in all instances, the most advanced in development, and the uppermost is often imperfectly developed. The tip of the rachilla, prolonged beyond the uppermost floret, ends in a sharp point which becomes hard and thornlike at maturity.

The indurated lemma covers the cavity in which the flower is located and is adnate to the rachilla except at the top (Fig. 11). The nature of this adnation is not wholly clear, but it seems that the lemma is really a tubular sheath around the flower, and this tube is adnate to the rachilla for the greater part of its length. I know of no other grass in which the lemma is tubular, but there seems to be no reason why it might not be. It is generally regarded as the sheath of a leaf, and vegetative leaf sheaths are often tubular.

The flower is functionally pistillate, but short rudiments of the three stamens are regularly present in both species. The style is divided into two parts only in the upper, stigmatic portion, the greater part of which is exserted from the tubular opening of the lemma. No lodicules have been observed, and, if they were present, they certainly could not perform their usual function, on account of the peculiar form of the lemma. The palea is thin and membranous, and the two keels are usually evident; but there are no vascular bundles.

Fournier's statement that there are two glumes, two paleae, and two lodicules (squamulae) cannot be reconciled with these observations, but it is possible, in part, to explain his statement. Apparently having no idea but that what we call a spikelet was a spike, he expected to find two glumes and interpreted the outer part of the lemma as one and the inner part as the other. The palea sometimes splits when dry material is dissected, and it is possible that these two parts were regarded as the two separate bracts which he expected to find. Microtome sections are a most helpful safeguard in interpreting dissections of these structures.

It is more difficult to explain Scribner's observation of a second flower, in some cases, above the one ordinarily seen. His Figure *e*, Plate 266, copied here as Figure 7, is very convincing except for the fact that I have found nothing of the kind in any of the material which I have examined. It seems hardly possible that, in dissecting dry material, he could have broken off a fragment which would have been so deceptive as to have resulted in the figure which he gives. Granting that the material which I have examined, and which was collected in one locality, may not have shown the full range of variation of the parts in question, I am forced to regard his figure with some skepticism until I have seen an actual specimen which will substantiate its accuracy.

There is a further question as to why the finding of this second flower did not have more influence upon Scribner's interpretation of the pistillate inflorescence. A second flower in the position indicated would constitute most convincing evidence that the structure was a spike, but, even after discussing this point, he goes counter to prevailing opinion and concludes

that it is a spikelet. In view of all these uncertainties, we cannot give much weight to this report until the observation is repeated.

In the inflorescence the position of these pistillate units corresponds exactly with that of entire *spikes* in the staminate plants, but they may be interpreted as spikes which have contracted to the point where only the terminal spikelet remains. A careful search for remnants of lost spikelets, or for a spike composed of two or more spikelets not subtended by prophylls, might yield positive results.

TAXONOMIC POSITION

Although the early investigators placed *Jouvea* in the Hordeae, this way of disposing of it has not been very satisfactory. The staminate spikes are much like the inflorescences of *Agropyron* or *Lolium*, and the pistillate inflorescences resemble externally the spike of *Lepturus;* but even if we were to grant that the pistillate structure were a spike, which now seems improbable, there would still be a question as to whether *Lepturus* were closely enough related to *Lolium* and *Agropyron* to make their respective resemblances to the two sexes of *Jouvea* significant.

Prat (1933) has recently made a special study of *Jouvea* in developing and applying a new criterion for the division of the grasses into two subfamilies. He finds certain correlations which lead him to believe that the epidermal cells and the trichomes of the leaves may be used as a guide, the trichomes of the Pooideae being unicellular, while those of the Panicoideae consist of two or more cells. On this basis, he takes *Jouvea*, not only out of the Hordeae, but even out of the Pooideae, and places it in the Panicoideae.

His observation of the trichomes of *Jouvea*, particularly those of the ligule, is correct; they are usually composed of two or more cells. But the queer alignments which result from the application of his method to the entire grass family (Prat, 1933) engender a serious doubt as to the value of this criterion of classification. If we are to take *Jouvea* out of the Hordeae, we must certainly hope for a better alternative than to place it in the Panicoideae.

According to Schwendener's method (1890) of separating the two subfamilies, *Jouvea* would be placed in the Pooideae. Both Prat's figures and the sections which I have made of leaf blades show the mestome sheath which Schwendener designates as a characteristic of that sub-family.

A few other tests of relationship may be mentioned in passing, although they cannot be given much weight until their application to general problems of grass phylogeny is better known. No chromosome counts have been reported for either species of *Jouvea*. The absence of auricles on

the leaves and the profuse branching of the culms are hard to reconcile with the Hordeae. The few seedlings of *J. pilosa* which have been grown show a definitely elongated "mesocotyl," while the short type is regarded as more characteristic of the Hordeae. The taxonomic significance of this character is weakened, however, by the fact that at least one genus of Hordeae, namely, *Lolium*, has the elongated mesocotyl. The leaf blades of both species show, near the middle or toward the distal end, a peculiar constriction which is apparently due to some restraining effect as the leaf expands in the bud (Figs. 8, 9). This same characteristic is so well developed in *Agropyron* that it is regularly employed by farmers as an aid in identifying quack grass (*A. repens*). This same characteristic has, however, also been observed in at least two species of the bamboos.

These conflicting factors make it still difficult to dispose of *Jouvea* in any very satisfactory way. If we exclude for the moment Prat's classification, which seems to make matters worse rather than better, the possibilities are reduced to the Hordeae and the Festuceae; and the choice between these two will be difficult to make until we know better the meaning of some of the differences which now separate the tribes.

For the present I should prefer to be guided by the absence of auricles, the branched culm, the staminate inflorescence, and the similarity to *Distichlis* and *Uniola* and place *Jouvea* in the Festuceae, regarding the pistillate inflorescence as the result of one of those erratic ventures in evolution which have apparently occurred in so many genera of grasses.

SUMMARY

The morphological evidences available at present indicate that the characteristic thorn-like structure in which the pistillate flowers of *Jouvea* are borne is a spikelet rather than a spike.

Each pistillate flower is deeply imbedded in the rachilla and covered by a tubular lemma which is adnate to the rachilla for the greater part of its length.

Nothing comparable with the second flower, above the functional one, as reported by Scribner, has been found in a large amount of material investigated. It is concluded that any interpretation depending upon this point should await a repetition of his observation.

The pistillate flower has three rudimentary stamens but no lodicules; the staminate flower has two lodicules but no rudiment of a pistil. The staminate spikelet is much like that of *Distichlis* and presents no serious morphological problem.

Without an exhaustive study of the differences between the Hordeae and the Festuceae it would be difficult to decide between the two as to the

proper place for *Jouvea*, but the weight of evidence at present favors placing it in the latter.

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The Taxonomy and Ecology of Agropyron spicatum and A. inerme

REXFORD F. DAUBENMIRE

During the course of intensive field work on prairie types where bluebunch wheatgrass dominates, the writer has made many observations which do not support the current taxonomic concepts of this grass.

The type specimen of *Agropyron spicatum* (Pursh) Scribn. and Smith (described in 1814) has long awns which are well reflexed from the spike. In 1897 Scribner and Smith described an awnless form of the species, then known as *A. divergens* Nees., calling it variety *inerme* and distinguishing it from the species by the awnless character alone. In 1909 Rydberg elevated the variety to the species *A. inerme* (Scribn. and Smith) Rydb.

Repeated observations in the field reveal every degree of intergradation between these allegedly distinct grasses. From completely awnless lemmas (*A. inerme*) one finds awns of any length up to about 2 centimeters. Frequently the lower spikelets on the inflorescence are totally awnless while the upper ones have awns varying from barely perceptible to a centimeter or more in length. Also one finds every intergradation from erect to strongly divergent awns. Usually the shorter the awn, the greater the tendency to remain erect as the spikelet matures, but instances where the reverse is true are common. The relative length of awns, as well as the degree of bending is fairly uniform for the same plant, but is scarcely identical on any two specimens.

Since the only character which distinguishes the members of this completely intergrading series is the nature of the awn, the group could be split into as many species, varieties, or forms as there are variations in awns. Hitchcock (1935), following the type specimens, called all awnless forms *Agropyron inerme*, and all forms with long divergent awns *A. spicatum*, while the intergrades apparently were not known to exist, for such specimens can not be keyed out nor are they mentioned under either species description. Tidestrom (1925) maintained the same distinction as Hitchcock but remarked the complete intergradation of the two extremes, In a recent manual to the flora of this region (St. John, 1937), the dividing line between the two "species" is placed so as to lump awnless with erect awned species under *A. inerme.*

The present status is quite unsatisfactory since (1) all forms which are known are not taken into account, and (2) a *completely intergrading* series of plants is arbitrarily split into *species* on a *single* character.

The writer is of the opinion that if the group is to be split, only two forms can be distinguished: (1) inflorescences in which none of the lemmas are awned, and (2) inflorescences in which some or all of the lemmas are

awned. Since both the characters of length and degree of bending vary without consistent relation to each other, the second group of variants must either be lumped under the same name, or else a dozen or more arbitrarily distinguished forms must be set up. The latter treatment would be unacceptable to most botanists.

If the forms are to be separated as above into the only two categories which can always be distinguished, the question arises as to whether they should be given specific rank similar to the present status, or whether they should be designated as the two most recognizable forms of the same polymorphic species.

A very strong point in favor of lumping all forms into the same species, aside from the complete morphological intergradation, is a peculiar yet identical physiological trait possessed by all forms. Under drier climates or more xeric edaphic conditions, all of these forms assume the bunch habit, but under a more mesic climate and on favorable soils the plants are always sod-formers and fruit less prolifically. According to current taxonomic viewpoints, the sod and bunch habits are fundamental and fixed characters of the species in this genus, for they are invariably used in keys to separate the species. If these characteristics are so fundamental, we have further evidence that this entire series of intergrading forms should be considered the same species, since all of them change from the bunch to the sod habit under conditions of a more favorable waterbalance of the environment,—an ability which no other species of the genus appears to have. It is remarkable that this sod habit has been so completely overlooked by taxonomists, for it has twice been described by plant ecologists (Weaver, 1917; Shantz, 1924).

Because of the complete intergradation of the awn character which forms the sole morphological basis of distinction, and because of the identical and unusual response to environmental variation in which the fundamental growth form is altered, the writer recommends that (1) a single species name (*Agropyron spicatum* (Pursh) Scribn. & Smith) be applied to the entire group, (2) the description of this species be broadened as follows to include all the variations now known: Some or all of the lemmas awned, awns erect to strongly divergent, varying in length from very short up to 20 mm. or more; plants of either the sod or bunch habit, (3) if any variant in the group is to be given nomenclatorial recognition, a single variety, differing from the species only by the complete absence of awns, be designated as *Agropyron spicatum* var. *inerme* Heller (see Hitchcock, 1935, p. 773).

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INDEX TO AMERICAN BOTANICAL LITERATURE

The aim of this Index is to include all current botanical literature written by Americans, published in America, or based upon American material; the word America being used in the broadest sense.

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BULLETIN
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The Genus Pholistoma Lilja[1]

LINCOLN CONSTANCE

(WITH ONE FIGURE AND PLATE 7)

The three species and one variety included in this paper have been segregated from *Nemophila* Nutt. and *Ellisia* L., respectively, because they are thought to constitute a natural group quite distinct from either of these two genera. The customary disposition of two of the species within *Nemophila* with plants radically unlike themselves, was based upon the assumption that the possession of intersepaloid bracts on the calyx was, in itself, a condition forming a trustworthy generic boundary to distinguish distinct and natural species-assemblages. Into *Ellisia*, on the other hand, was placed the third species, chiefly because it lacked the characteristic auricles of *Nemophila.*

Thus were separated closely related forms which agree overwhelmingly in their distinctive succulent and scandent or reclining habit, their prickly stems and spiny capsules, the regular markings of their ecucullate globose seeds, and their geographical distribution. Even though a considerable upheaval in nomenclature necessarily results, this separation does violence to avowed aims of phylogenetic taxonomy, or systematic botany, and must be corrected. Greene (1894) was apparently the first writer to perceive the close affinity between these species. Accordingly, he combined them under *Nemophila*. In this position, however, they form a unit whose aberrant features jeopardize the homogeneity of that genus. *Ellisia* would be similarly affected were they all to be placed in that group.

The definite pattern of the seed coat, the absence of a cucullus and the enlargement of the persistent calyx in fruit relate *Pholistoma* to *Ellisia*, proper. *Ellisia Nyctelea*, however, has a delicate, non-succulent, non-scandent habit, lacks the prickles on the stem and capsule, has a short and narrow corolla usually shorter than the calyx, and differs fundamentally in geographical range. All of these conditions indicate that the existing

[1] Part of the expense of publication borne by the author.

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discrepancy between the two genera demands consideration. The several-flowered, secund, cymose inflorescence of *Pholistoma* finds a counterpart in that of *Eucrypta* Nutt., but the distinctive features of that genus, already pointed out (Constance, 1938), preclude the incorporation of these two groups. The only species to share the prickly armature of the stem with *Pholistoma* is *Nemophila breviflora* Gray, which has cucullate, pitted seeds and other divergent characters which argue strongly against any close relationship.

It has been proposed (Constance, 1939) to take up *Pholistoma* Lilja, and to erect it as a genus embracing the segregated elements in question. Although this name is infrequent in botanical literature, it was validly published and adequately identified by a type species and so is the mandatory designation for the group if it is not to be retained in either *Ellisia* or *Nemophila*. Lilja, in founding this genus, laid stress upon the angled corolla-tube and broad corolla-scales of *Pholistoma auritum*, the type species. These characters have, apparently, only specific value. The name is derived from the Greek words, *pholis*, a scale, and *stoma*, a mouth, in reference to the fact that the squamae sometimes conspicuously occlude the mouth of the corolla-tube. This treatment, it is believed, will adequately circumscribe and define a natural alliance of species and, at the same time, relieve both *Ellisia* and *Nemophila* of species whose inclusion would merely serve to destroy their genetic unity.

The present geographical distribution of the species may afford a clue to the origin of the genus. The range of *Pholistoma racemosum* and *P. membranaceum*, and the combined ranges of *P. auritum* and var. *arizonicum*, are largely comparable to those of several living species represented by fossil equivalents in the Miocene Tehachapi Flora. Axelrod (1939) attributes a northern Mexican origin to these modern species. It is not improbable that *Pholistoma* may have developed in this area and later spread to the north and east to occupy its present range.

The writer is indebted to Dr. W. L. Jepson for the opportunity of examining critical specimens in his working herbarium of the Californian flora, and to Dr. Mildred E. Mathias and others for the gift of a number of significant collections. Professor Milo S. Baker, Kenwood; Mr. Ira W. Clokey, South Pasadena; Dr. Robert F. Hoover, Berkeley; and Mr. Frank W. Peirson, Altadena, have generously made avilable the specimens of this genus in their private herbaria. The curators of the following important collections have kindly loaned for study the specimens in their care: California Academy of Sciences, San Francisco (CA); Cornell University, Ithaca (CU); Field Museum of Natural History, Chicago (F); Gray Her-

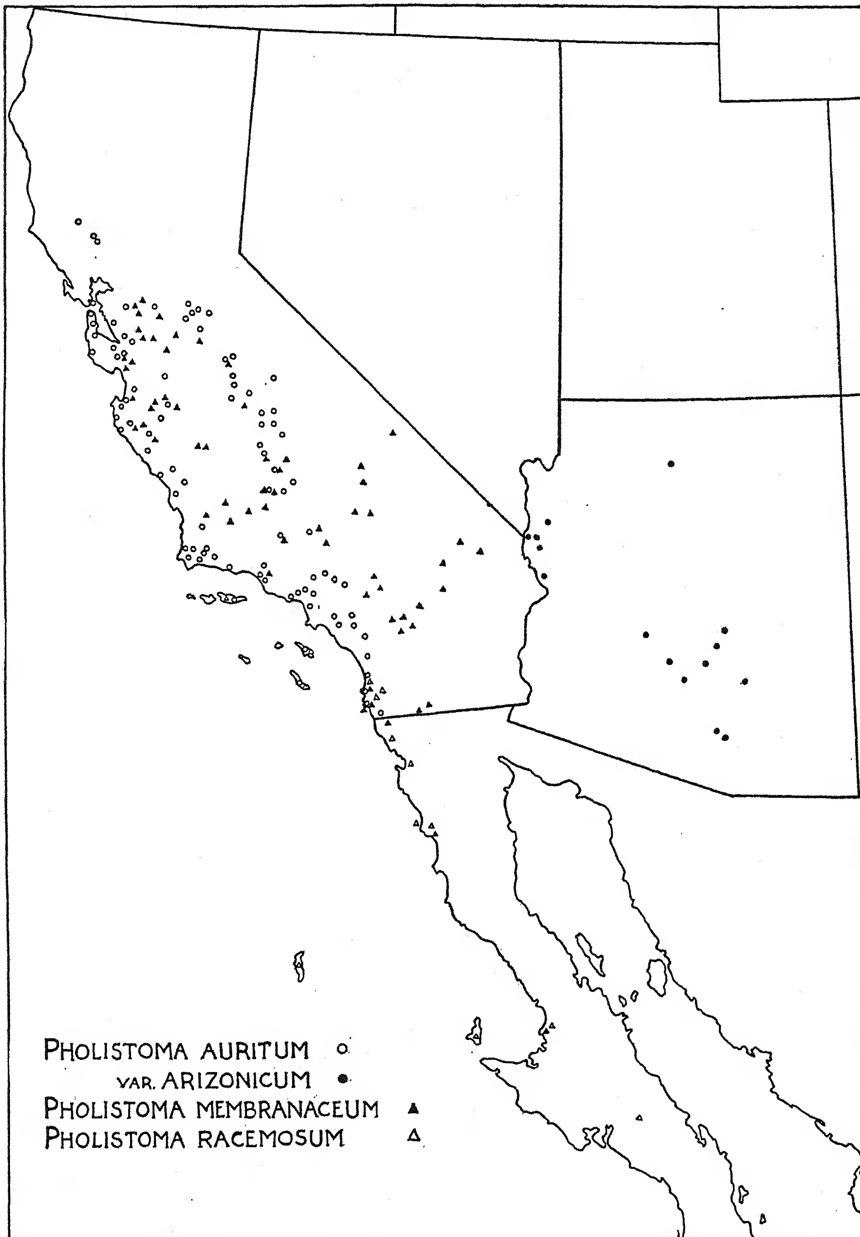


Fig. 1. Geographical Distribution of *Pholistoma*.

barium of Harvard University, Cambridge (G); Royal Botanic Gardens, Kew (K); Missouri Botanical Garden, St. Louis (M); New York Botanical Garden, New York (NY); Oregon State College, Corvallis (OS); Pomona College, Claremont (P); Academy of Natural Sciences, Philadelphia (PA); Rocky Mountain Herbarium of the University of Wyoming, Laramie (RM); Dudley Herbarium of Stanford University (S); University of California, Berkeley (UC); University of Oregon, Eugene (UO); United States National Herbarium, Washington (US); University of Washington, Seattle (UW); Vegetation Type Map Herbarium of the California Range and Forestry Experiment Station, Berkeley (VTM); State College of Washington, Pullman (WS).

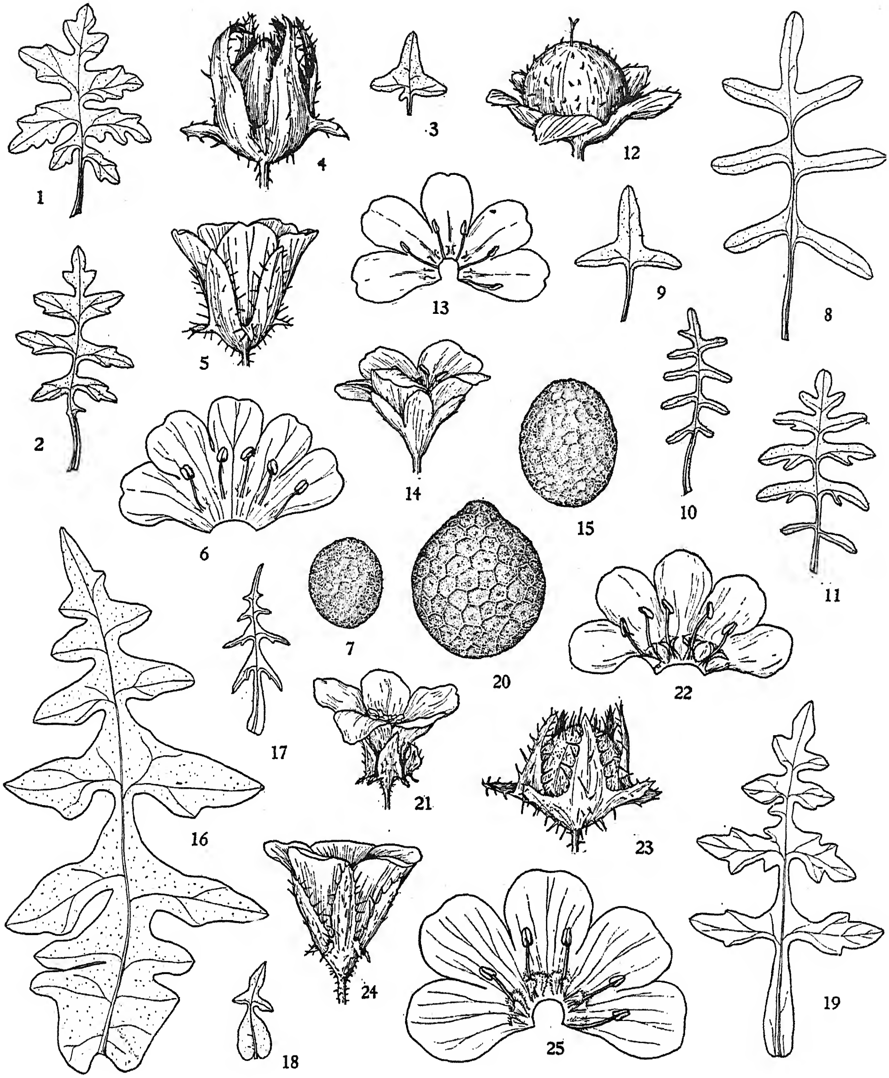
TAXONOMIC TREATMENT

PHOLISTOMA Lilja

Pholistoma Lilja; in Lindblom, Bot. Notiser, 40. 1839.

Nemophila Nutt., *Ellisia* L., *Macrocalyx* Trew, and *Nyctelea* Scop., all of subsequent writers, in part, not of the original authors!

Green or glaucous succulent annual herbs, at first simple, but soon much branched and reclining upon other plants or upon the ground. Stems succulent and brittle, angled and the angles armed with unciniate prickles, hispidulous or glabrate. Cotyledons with an oval or orbicular blade, truncate at base, on slender petioles of greater length, usually deciduous before full anthesis. Lowest leaves opposite, the others alternate, oblong, ovate-lanceolate or ovate-deltoid, cordate or truncate at base and pinnately divided into lanceolate. oblong or ovate acute or obtuse lobes which are entire or few-toothed, slightly succulent or thin and membranous, venose, more or less hispidulous on both surfaces and bristly or prickly on the margins and on the veins below; uppermost leaves reduced and short-petioled, often deltoid, 3-lobed; stomata confined to the paler lower surface or a few on the veins above; petioles narrowly or broadly winged, slightly dilated and connate-clasping at the base or broadly flaring and auriculate, equalling or shorter than the blades. Flowers solitary in the axils or several in few-bracteate, semi-secund, raceme-like cymes which arise in the axils or opposite the alternate leaves or terminally. Calyces broadly campanulate, 5-cleft nearly to the base into linear-lanceolate to oval acute or obtuse lobes, these more or less hispidulous on both surfaces and bristly-ciliate; sinuses provided with auricles resembling the sepals in form, or sinuses naked. Corollas bowl-shaped or semi-rotate, white, blue or violet, the oval to obovate lobes exceeding the tube, the whole exserted from the calyx; corolla-scales a pair at the base of each filament, broad and triangular or narrow or minute, a nectary between each pair. Stamens included but slightly exceeding the corolla-tube, anthers oblong- or ovate-cordate. Pollen grains smooth, tricolpate. Styles cleft less than one-half. Mature capsules globose, armed with stout bristles



CONSTANCE: PHOLISTOMA

Explanation of Plate 7.

Figs. 1–7. *P. racemosum:* Figs. 1–3, leaves $\times\frac{1}{2}$; Fig. 4, fruiting calyx $\times 3$; Figs. 5, 6, corolla $\times 3$; Fig. 7, seed $\times 7\frac{1}{2}$.

Figs. 8–15. *P. membranaceum:* Figs. 8–11, leaves $\times\frac{1}{2}$; Fig. 12, fruiting calyx $\times 4$; Figs. 13, 14, corolla $\times 3$; Fig. 15, seed $\times 7\frac{1}{2}$.

Figs. 16–23. *P. auritum:* Figs. 16–19, leaves $\times\frac{1}{2}$; Fig. 20, seed $\times 7\frac{1}{2}$; Figs. 21, 22, corolla $\times 1$; Fig. 23, fruiting calyx $\times 2$.

Figs. 24, 25. *P. auritum arizonicum*, corolla $\times 3$.

or prickles, exceeded by the enveloping or stellate-spreading, strongly accrescent calyx, loculicidally dehiscent by two valves. Seeds mostly 1–6, homomorphic, globose, light brown, regularly alveolate or reticulate. Cucullus none. Type species: *Pholistoma auritum* Lilja (*Nemophila aurita* Lindl.).

KEY TO THE SPECIES

Foliage green; calyx with conspicuous auricles, enveloping the mature capsule; capsule 5–10 mm. in diameter.
  Cauline leaves auriculate-clasping; corolla-scales broad and conspicuous.
    Corolla usually 1–3 cm. broad; California . . . . *P. auritum.*
    Corolla usually less than 1 cm. broad; Arizona . . . . var. *arizonicum.*
  Cauline leaves with narrowly winged but only slightly connate petioles; corolla-scales usually narrow and inconspicuous; corolla mostly less than 1 cm. broad . . . . *P. racemosum.*
Foliage glaucous; calyx without auricles, stellate-rotate under the mature capsule; capsule 2–4 mm. in diameter . . . . *P. membranaceum.*

PHOLISTOMA AURITUM (Lindl.) Lilja

Nemophila aurita Lindley, Bot. Reg. **19:** t. 1601. 1833.
Pholistoma auritum Lilja; in Lindblom Bot. Notiser, 40. 1839.
Viticella aurita Macbride, Contr. Gray Herb. **59:** 29. 1919.

Foliage green; stems 2–12 dm. long. sparingly hispidulous; blades of the cotyledons 8–10 mm. in diameter; lower leaves oblong to ovate-lanceolate, 8–15 cm. long, 2–8 cm. broad, acuminate at apex, cordate at base, divisions 7–13, oblong or lanceolate, falcate or retrorse, obtuse or acute, entire or 1–5-toothed, more or less hispidulous on both surfaces; petioles broadly winged and auriculate-clasping; flowers solitary or 2-6 in cymes; calyx-lobes lanceolate or ovate-lanceolate, 4–8 mm. long, 2–2.5 mm. broad, auricles similar, 1–2 mm. long, corolla 1–3 cm. broad, lavendar to blue or violet with darker markings at the throat, the oval or obovate lobes somewhat erose and often pubescent distally, the short tube paler, angled and slightly coarctate at the throat; corolla-scales purple, 3-angular, the free edge often fimbriate, the yellow nectaries conspicuous; anthers 1.5 mm. long; style about 5 mm. long; capsule 5–10 mm. in diameter, enclosed by the calyx; seeds 1–4, 2–3 mm. in diameter.

Type locality: "found in California," *Douglas.*

Range: Coast Ranges of California from San Diego County to San Francisco Bay and Lake County; San Clemente and Santa Catalina islands; Sierra Nevada foothills from Kern County to Calaveras County; Upper Sonoran and Arid Transition life zones.

Representative material: CALIFORNIA. Locality uncertain: "California," *Douglas* (K: type of *Nemophila aurita*, G,NY), *Bridges 170* (G,NY,UC, US); without locality, *Coulter 471* (G,K). Lake Co.: Clear Lake, 1933, *M. S. Baker 7518* (Baker,CA); Sulphur Banks, 1901–2, *Bowman 270* (G,S). Marin Co.: Angel Island, *Rattan* (S), 1888, *Chesnut* (UC). Contra Costa Co.: Alamo Canyon, 1932, *Bowerman 1089* (UC); Lake Chabot,

1904, *Osterhout & Gardner* (UC). Alameda Co.: Niles Cañon, 1891, *Chesnut & Drew* (P,UC,UO); Oakland, 1860–7, *Bolander 152* (F,M); San Leandro, 1877, *H. Edwards* (CA,NY); Sunol, 1938, *Constance 2231*. San Francisco Co.: South San Francisco, 1892 *E. Cannon* (CA). San Mateo Co.: Burlingame, 1925, *J. Campbell* (CU); Pescadero Creek, 1928, *C. Meyer 376* (UC). Santa Clara Co.: Stanford University, 1902, *Abrams 2309* (G,M, NY,P,RM,S), 1902, *C. F. Baker 399* (CA,F,G,M,NY,P,RM,S,UC,US, WS); Stevens Creek, 1907, *Heller 8516* (F,G,M,NY,PA,S,US). Monterey Co.: Abbotts, 1938, *Constance & Hoover 2060;* Del Monte, 1903, *Heller 6683* (CA,F,G,M,NY,P,PA,RM,S,UC,US); Santa Lucia Mountains, 1898, *Plaskett 81* (G,NY,US). San Benito Co.: Pinnacles, 1929, *Mexia 2364* (CA, UC,US); Tres Piños River, 1921, *Abrams & Borthwick 7845* (S). San Joaquin Co.: Stockton, *Stanford 188* (UC). Stanislaus Co.: Knights Ferry, 1938, *Constance 2195;* Modesto, 1935, *Hoover 369* (Hoover, UC). Merced Co.: Pacheco Pass, 1925, *Abrams 10747* (S), 1938, *L. Koch 159* (Baker, UC) Calaveras Co.: Robinson's Ferry, 1854, *Bigelow* (G,NY,PA,US); Table Top Mountain, 1936, *Belshaw 1897* (VTM). Tuolumne Co.: Columbia, 1916, *A. L. Grant 679* (Jepson); Iron Cañon, 1919, *Ferris 1661* (CA,NY, S,US). Mariposa Co.: Mariposa Creek, 1938. *Constance & Mason 2128;* Pea Ridge Road, 1903, *Congdon* (US). Madera Co.: Kelshaw Corners, 1938, *Constance 2201;* Pollasky, 1906, *Heller 8147* (CA,F,G,M,NY,PA,S, US). Fresno Co.: Squaw Valley, 1938, *Constance 2224;* Tollhouse, 1938, *Constance 2214*. Tulare Co.: Exeter, 1930, *Parks & Parks 0423* (CA,M, NY,P,UC), 1938, *Constance & Mason 2105;* Oak Grove, 1925, *Bacigalupi 1217* (NY,P,S). Kern Co.: Caliente, 1938, *Mathias 1344* (UC); Hobo Hot Springs, 1938, *Constance & Mason 2119;* Kern Canyon 1938, *Mathias 1346* (UC). San Luis Obispo Co.: Cambria, 1926, *Eastwood 13609* (CA); San Luis Obispo, 1882, *Summers* (UC,US). Santa Barbara Co.: Dos Pueblos, 1861, *Brewer 396* (UC,US); Los Alamos Creek, 1920, *Jepson 8449* (Jepson); Santa Barbara, 1902, *Elmer 3942* (M,NY,P,S,US); "St. Barbara," *Nuttall* (K,PA); Santa Cruz Island, 1888, *T. S. Brandegee* (UC), 1930, *Abrams & Wiggins 109* (CA,F,G,S,UC). Ventura Co.: Casitas Pass, 1902, *H. M. Hall 3136* (NY,S,UC,UO,US); East Casitas Pass, 1931, *C. Wolf 2032* (S,UC). Los Angeles Co.: Claremont, 1917, *Johnston 1249* (Clokey,P,S); Los Alisos Canyon, 1931, *Epling* (CA,M,OS,S,UC,US); Los Angeles, 1888–9, *Hasse* (M,NY,S); Los Flores Canyon, 1930, *Epling & Ellison* (M,OS,PA,UC,US); Mandeville Canyon, 1929, *Clokey & Templeton 4437* (Clokey,CU,G,M,NY,P,UC), 1930, *Epling* (F,M,OS,UC,US); "Pueblo de los Angeles," *Gambel* (G); San Clemente Island, 1903, *Trask 201* (NY,US), 1923, *Munz 6663* (P,UC); Santa Catalina Island, 1901, *Trask 456* (F,NY), 1904, *G. B. Grant 832* (G,M,RM). Orange Co.: Santa

Ana Cañon, 1926, *M. E. Jones* (G,S); Silverado Cañon, 1920, *Munz & Harwood 3725* (P,US). Riverside Co.: Murietta, 1916, *Robinson & Crocker* (M,P); Prado, 1920, *Barrus & Whetzel 249* (CU). San Diego Co.: Fallbrook, 1882, *M. E. Jones 3095* (CA,Clokey,M,NY,P,S,US); La Jolla, 1914, *Clements & Clements 96* (F,G,M,NY,PA); San Diego, 1850, *Parry* (NY,US), 1916, *Spencer 107* (G,NY,UC,US); San Pasqual, 1852, *Thurber 604* (F,G,NY); Ysidora, 1903, *Abrams 3290* (F,G,M,NY,P,PA,S,US).

The plants vary greatly in size, foliage, corollas and fruits, but except var. *arizonicum* no variant populations have, as yet, been described. The stems often attain a great length, climbing up through and over shrubs by means of their efficient recurved prickles. The almost rotate limb, angled tube and conspicuous nectaries give this species a striking appearance. The color of the corolla fluctuates over a wide range of hues and intensities, from very pale to deep blue, and from light to dark violet.

To date, no specimens of *P. auritum* have been reported from Mexico, although it occurs so close to the international boundary as to make its subsequent discovery in Baja California highly probable.

Pholistoma auritum var. **arizonicum** (M. E. Jones) n. comb.

Nemophila arizonica M. E. Jones, Contr. West. Bot., **12:** 50. 1908.

N. aurita var *arizonica* Brand, Pflanzenr. IV. 251. 45. 1913.

Closely similar to the species, but usually smaller, more slender and less prickly throughout; divisions of the leaves fewer and very blunt; corollas usually less than 1 cm. broad, about equalling the calyx.

Type locality: "Chimihuevis Mountains, Arizona" (Mohave County), 1903, *M. E. Jones*.

Range: mountains of western and south-central Arizona.

Representative material: ARIZONA. Mohave Co.: Chimihuevis Mountains, 1903, *M. E. Jones* (P: type of *Nemophila arizonica*); Fort Mohave, 1884, *Lemmon* (UC); Yucca, 1884, *M. E. Jones* (P,PA). Coconino Co.: Diamond Creek Cañon, 1893, *Wilson* (UC); Hermit Creek, 1917, *Eastwood 6024* (CA). Gila Co.: Roosevelt Dam, 1917, *Eastwood 6259* (CA); Winkelman, 1922, *Wiegand & Upton 4080* (CU). Maricopa Co.: Salt River Mountains, 1932, *Gillespie 8849* (G,S,UC,US); Stewart Mountain, 1935, *Peebles 10656* (F,US); Tortilla Flat, 1935, *Nelson & Nelson 1761* (M,NY,RM); White Tank Mountains, 1932, *Gillespie 8876* (NY,P,S,US). Pinal Co.: Desert Wells—Stewart Mountain, 1932, *Gillespie 5451* (NY,P, S,UC,US); Superstition Mountain, 1937, *Peebles, Harrison & Kearney 3704* (US). Pima Co.: Alamo Well, 1933, *Wiggins 6527* (S,US); Sierra Tucson, 1884, *Pringle* (F,G,M,NY,PA,UC,US).

The consistently smaller and often paler corollas, the blunt leaf-lobes, and the Arizonan distribution mark this as a valid geographical variant of *P. auritum* and warrant its retention in varietal status. The size of the flowers suggests those of *P. racemosum*, with which it has sometimes been confused, but the flaring petioles and broad scales relate it to *P. auritum.* Despite the sharp discontinuity in distribution between the species and its variety, morphological agreement is too close to allow of specific separation.

Pholistoma racemosum (Nutt.) n. comb.

Nemophila racemosa Nuttall ex Gray, Proc. Amer. Acad. **10:** 315. 1875.

Viticella racemosa Macbride, Contr. Gray Herb. **59:** 30. 1919.

Nemophila erodiifolia Millspaugh ex Millspaugh & Nuttall, Field Mus. Publ. 312. Bot. Ser. **5:** 205. 1923.

Foliage green; stems 3–6 dm. long, sparingly hispidulous or glabrate; blades of the cotyledons 6–9 mm. in diameter; lower leaves ovate or deltoid-ovate in outline, 4–10 cm. long, 2–6 cm. broad, obtuse at apex, subcordate or truncate at base, divisions 5–9, oblong or ovate, obtuse or acute, entire or 3–5-toothed, more or less hispidulous on both surfaces, more densely so beneath; petioles narrowly winged and not auriculate; flowers solitary or usually 2–6 in cymes; calyx-lobes linear- or ovate-lanceolate, 2–3 mm. long, 1–1.5 mm. broad, auricles similar, 1–1.5 mm. long; corolla 0.6–1 cm. broad, white or blue, the obovate lobes often pubescent distally; corolla-scales 3-angular but usually narrow or obsolete, the upper portion often free and fimbriate; anthers 0.6 mm. long; style about 2.5 mm. long; capsule 5–8 mm. in diameter, enclosed by the calyx; seeds usually 4–6, sometimes solitary, 1–2 mm. in diameter.

Type locality: "California; San Diego, *Nuttall.*"

Range: San Diego and Baja California coast; Santa Cruz, San Clemente, Santa Catalina, San Martin, Cedros and Guadalupe islands.

Representative material: CALIFORNIA. Santa Barbara Co.: Santa Cruz Island, 1888, *T. S. Brandegee* (F,UC), 1930, *Abrams & Wiggins 1* (CA,F, G,S,UC), 1930, *Clokey 5033* (Clokey,G,NY). Los Angeles Co.: San Clemente Island, 1885, *Nevin & Lyon* (G,S), 1903, *Trask 200* (NY,US), 1923, *Munz 6646* (G,P,UC). Santa Catalina Island, 1893, *McClatchie 349* (F, NY), 1900–4, *G. B. Grant 831* (F,G,M,PA,RM,S,UC), 1920, *Millspaugh 4687* (F: type of *Nemophila erodiifolia*), 1921, *E. C. Knopf 13* (F,US). San Diego Co.: La Jolla, 1914, *Clements & Clements 97* (F,G,M,NY,PA), 1929, *Parks & Parks 0339* (CA,G,M,NY,P,RM,S,UC); Mission Hills, 1903, *Abrams 3431* (G,M,NY,P,S); Point Loma, 1913, *Eastwood 2563* (CA, Clokey, G,NY,US); San Diego, 1882, *M. E. Jones 3056* (CA,Clokey,G, M,NY,P,US); "St. Diego," *Nuttall* (G: type of *Nemophila racemosa*, K): Tia Juana, 1913, *Eastwood 2922* (CA,G,US).

BAJA CALIFORNIA. San Quintin, 1935, *Epling & Robison* (NY,S,UC); Santo Domingo, 1930, *Wiggins 4294* (NY,S,UC), *4506* (S,UC); Todos Santos Bay, 1885, *Orcutt 1259* (G,M,US); Cedros Island, 1897, *T. S. Brandegee* (NY,UC); San Martin Island, 1897, *Anthony 229* (G,M,S,US); Guadalupe Island, 1875, *Palmer 76* (M,NY,PA), 1889, *889* (G,US), 1885, *Greene* (G,S,UC), *Anthony 254* (F,G,M,P,S,UC,US), 1892–3, *Franceschi 32* (F,M,UC,US), 1911, *J. N. Rose 16017* (NY,US).

Nemophila erodiifolia was separated because it had blue or bluish, instead of white corollas and more than one seed in each capsule instead of solitary seeds. Perhaps the emphasis upon seed-number was due to Brand's belief that *P. racemosum* always has only one seed in each capsule, although some of the specimens he cites show as many as eight or nine seeds. Color of the corolla is notoriously variable in the entire tribe and so cannot lend weight to this segregate, which is without taxonomic significance.

Pholistoma membranaceum (Benth.) n. comb.

Ellisia membranacea Bentham, Trans. Linn. Soc. Lond. **17:** 274. 1834.
Macrocalyx membranaceus O. Kuntze, Rev. Gen. **1:** 434. 1891.
Nemophila membranacea Greene, Man. Bay-Reg., 252. 1894.
Ellisia membranacea var. *hastifolia* Brand, Pflanzenr. IV. 251. 38. 1913.
Nyctelea membranacea Tidestrom, Proc. Biol. Soc. Wash. **48:** 42. 1935.

Foliage glaucous; stems 0.5–6 dm. long, glabrous; blades of the cotyledons usually 4–7 mm. in diameter; lower leaves oblong to oval, 3–12 cm. long, 1–5 cm. broad, obtuse at apex, subcordate or truncate at base, divisions 5–11, oblong, obtuse, rather distant and entire or with a single broad lateral tooth, sparsely hispidulous on both surfaces; petioles more or less winged but not auriculate; flowers 2–10 in cymes, or rarely solitary: calyx-lobes oval, 2–3 mm. long, 1–2 mm. broad, obtuse, auricles 0; corolla 0.4–1 cm. broad, white and often with a lanceolate purple spot on each lobe, the lobes oval; corolla-scales 3-angular, very small and entire; anthers 0.4–0.6 mm. long; style 1.5–2 mm. long; capsule 2–4 mm. in diameter, the fruiting calyx stellate-spreading beneath it; seeds 1–2, 2–3 mm. in diameter.

Type locality: "from Mr. Douglas' Californian collection."

Range: Coast Ranges from Baja California to Contra Costa County; Sierra Nevada foothills from Mariposa County south and east through the desert ranges to Inyo and San Bernardino counties; absent from the islands and usually from the immediate coast; Upper and Lower Sonoran life zones.

Representative material: CALIFORNIA. Locality uncertain: "California," 1833, *Douglas* (K: type of *Ellisia membranacea*, G), *Coulter 470* (G,K,NY); "Southern California," 1876, *Parry & Lemmon 257* (F,NY). Contra Costa Co.: Antioch, 1868–9, *Kellogg & Harford 788* (CA,G,NY-

part); Nortonville, 1929, *Mason 5046* (UC). Alameda Co.: Cedar Mountain, 1903, *Elmer 4438* (CA,M,NY,OS,P,S,UC,UO,US: isotypes of *Ellisia membranacea* var. *hastifolia*); Corral Hollow Road, 1930, *Stanford 1397* (CA,G,M); Patterson Pass, 1933, *L. S. Rose 33057* (CA,F,M,P,S,UC). Santa Clara Co.: Edenvale, 1917, *Abrams 6400* (Clokey,NY,P,S,UW); Evergreen, 1893, *Davy 52* (RM,S,UC); Pacheco Pass, 1938, *L. Koch 158* (Baker,UC). Monterey Co.: Big Pinnacles, 1925, *Ferris 4120* (P,S); Jamesburg, 1929, *Mason 5039* (UC), 1938, *Constance & Hoover 2054;* Jolon, 1935, *Wiggins, 8029* (S,UC). San Joaquin Co.: Castle Rock, 1938, *Hoover 2792* (Hoover,UC). Stanislaus Co.: Arroyo del Puerto, 1935, *Sharsmith & Sharsmith 1553* (UC), *Ferris 9051* (CA,NY,S,UC); LaGrange, 1937, *Hoover 1706* (Hoover,UC). San Benito Co.: Emmet—Panoche Pass, 1921, *Abrams & Borthwick 7908* (NY,P,S); Gabilan Range, 1938, *Constance & Hoover 2065;* Glaucophane Ridge, 1938, *Constance & Hoover 2072;* The Pinnacles, 1930, *J. T. Howell 4616* (CA,G,US). Mariposa Co.; Lewis, 1892, *Congdon* (S). Fresno Co.: Alcalde, 1891, *T. S. Brandegee* (UC,US); Alcalde Canyon, 1938, *Hoover 2944* (Hoover,UC); Jacalitos Canyon, 1931, *J. T. Howell 5823* (CA). Tulare Co.: Exeter, 1930, *Parks & Parks 0436* (UC,US), 1938, *Constance & Mason 2102;* Middle Tule River, 1892, *Purpus 5080* (G,UC,US). Kern Co.: Caliente, 1905, *Heller 7612* (F,G,M, NY,P,PA,S,UC,US); Fort Tejon, 1857–8, *Xantus 88* (G,NY,PA,US); Kern River Canyon, 1938, *Mathias 1320* (UC), *1321* (UC), *1322* (UC); Tehachapi Pass, 1925, *Munz 8978* (P,UC). Inyo Co.: Funeral Mountains, 1891, *Coville & Funston 332* (CU,G,M,NY,PA,S,US); Great Falls Canyon, 1930, *Epling, Ellison & Anderson* (F,OS,US). San Bernardino Co.: Bonanza, 1920, *Munz & Harwood 3430* (P,US); Kelso, 1906, *M. E. Jones* (G,P,S); Lava Mountains, 1938. *Constance & Mason 2113;* Morongo Valley, 1928, *J. T. Howell 3404* (CA,G,NY,S,US). San Luis Obispo Co.: Bitterwater Valley, 1932, *Wiggins 5798* (NY,P,S,UC); Cuyama, 1896, *Eastwood* (G,UC); Paso Robles, 1938, *Constance 2085*. Ventura Co.: Road to Ojai, 1935, *Munz 13597* (P,S,UC). Los Angeles Co.: Antelope Valley, 1895, *Davidson* (S). Riverside Co.: Cabezon, 1881–3, *Parish & Parish 21* (F,Jepson,M,NY,PA,S,UC,UO,US,WS); Palm Canyon, 1930, *Spencer 1582* (G,P); Tahquitz, 1919, *Peirson 981* (Peirson); Whitewater, 1881, *Vasey* (PA,UC). San Diego Co.: Bernardo, 1903, *Abrams 3375* (F,G,M, NY,P,PA,S,UC,US); Coyote Cañon, 1902, *H. M. Hall 2813* (M,NY,S,UC, US); La Jolla, 1904, *Chandler 5129* (NY,S,UC); Ocean Beach, 1917, *Spencer 276* (G,NY,P); San Diego, 1849–50, *Parry* (NY,PA,US), 1875, *Palmer 244* (F,M), 1882, *M. E. Jones 3082* (Ca,Clokey,G,M,NY,P,S,US), *Pringle* (F,G,UO,US); "St. Diego," *Nuttall* (PA).

Baja California. San Quintin, 1889, *Palmer 638* (CA,F,G,NY,PA, US); Santo Domingo, 1930, *Wiggins 4288* (NY,S,UC); Tia Juana, 1882, *Orcutt 295* (US).

Variety *hastifolia* is a sporadic and trivial foliar variant without either correlated characters or geographical significance and is hence of no taxonomic worth. *P. membranaceum* agrees closely with the preceding species in habit, foliage and seeds, but its usually more complex inflorescence and its rotate fruiting calyx, without any trace of auricles, render it somewhat anomalous and give it a superficial resemblance to *Eucrypta*. Equally at home in the live-oak belt of the inner south Coast Ranges and with *Larrea* in desert areas, this species has occupied a range which is more definitely interior than that of either *P. auritum* or *P. racemosum*.

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Secondary Vascular Tissues of the Oaks Indigenous to the United States—I. The Importance of Secondary Xylem in Delimiting Erythrobalanus and Leucobalanus

SIMON WILLIAMS

(WITH SIX FIGURES)

INTRODUCTION

The original objective sought in this research was to determine whether it was practicable to attempt the identification of the species of *Quercus* native to the United States, on the basis of anatomical variations occurring in the secondary xylem; some progress has been made in this direction, and these results will be published at a later date. As the study of oak woods has progressed, however, it has become increasingly evident that considerable confusion exists in the taxonomy of the genus, a situation which has been further emphasized through the compilation of certain anatomical data, the seeming logical interpretation of which is in direct variance with existing classification. The present paper has been written in the hope that it may be of some service in clarifying the taxonomy of the genus.

If the identification of the various species of oak on the basis of wood structure is to be followed to its logical conclusion, it is patent that a trustworthy classification of the species within the genus must be available which can serve as a logical starting point. Furthermore, to reap the greatest benefits from the study, this classification must be one accepted by all leading taxonomists. A survey of the literature (4, 5, 6, 12, 17, 18, 19, 20, 24) has revealed that no such situation exists, that the taxonomy now employed in *Quercus* has inordinately magnified the natural complexities of this large group. The following paragraphs will serve to show the situation as it now exists in so far as it is concerned with the limits of subgenera.

CONCEPTS OF SUBGENERA IN QUERCUS

The concept of subgenera in *Quercus* is of genuine value, and certain natural groups of species within the genus have long been recognized by systematists (8, 19). As interpreted at present, two of these, ERYTHROBALANUS Spach, and LEUCOBALANUS Engel. (the red and white oaks, respectively), include all of the species native to the United States. CYCLOBALANUS Endl., CYCLOBALANOPSIS Benth. & Hook., and CHLAMYDOBALANUS Endl., are restricted to the Orient and hence do not fall within the scope of this paper.

With the concept of ERYTHROBALANUS and LEUCOBALANUS there is no dispute. The confusion exists, rather, in the efforts made to define the

boundaries of these subgenera, and in assigning species to them. The red and white oaks originally were grouped in LEPIDOBALANUS by Endlicher. Later Spach and then Liebmann, among others, split off ERYTHROBALANUS. In 1877, Engelmann (8) place the oaks in two sub-sections, LEUCOBALANUS (white oaks) and MELANOBALANUS[1] (black oaks); his paper is of particular interest since it serves to emphasize the difficulties that have always confronted systematists in selecting a set of characters that would successfully delimit the two natural groups and avoid flagrant exceptions. For example, Engelmann found it quite difficult to orient satisfactorily certain species in a manner at once logical and at the same time retain their natural affinities. Thus, LEUCOBALANUS, defined as having basal or rarely lateral abortive ovules, 6 to 8 stamens, sessile or subsessile stigmatic surfaces, and the inner surface of the acorn shell glabrous or rarely tomentose, includes in Engelmann's first arrangement such a species as *Q. emoryi* Torr. In a subsequent grouping later in the same paper, this species is listed with the black oaks, defined as having apical abortive ovules, 4 to 6 stamens, elongated recurved styles, and the inner surface of the acorn shell tomentose. Nevertheless, Engelmann's astuteness should not be overlooked for, despite the paucity of his species complement, he did so define the two subgroups that no exceptions occurred as regards any major definitive feature. Mention should be made at this time that Engelmann, either by design or by accident, failed to use acorn maturation as a major feature in separating the two groups, relegating this feature to secondary rank, common to both. It is difficult to understand why taxonomists since 1877 have deliberately altered Engelmann's concept of subgeneric limits, in this way creating an anomalous situation which cannot but cast considerable suspicion upon the validity of the present groupings.

A careful examination of the features now generally used in defining the limits of LEUCO- and ERYTHROBALANUS reveals the fact that no one character is used which is not duplicated in one or more species in the alternate subgenus. Taxonomists, by readjusting the emphasis to be placed on the various features listed by Engelmann, and by shifting various species between the two subgenera, have created exceptions that defeat the logic of the rule. The situation can best be stressed by resorting to an illustration, the interpretation of which calls for a summation of the features which, at present, characterize the red and white oaks, respectively.

CRITICAL ANALYSIS OF TABLE 1

Attention may now be focussed to advantage on the position accorded *Q. emoryi* Torr. and *Q. agrifolia* Nee, by taxonomists. With the exception

[1] ERYTHROBALANUS is commonly used in defining this group at the present time.

of Trelease's work (9), modern references list *Q. emoryi* as a white oak; *Q. agrifolia* is a red oak by unanimous consent. The logic of this procedure is open to question. *Q. emoryi* matures its acorn in one year, but the same holds for *Q. agrifolia*. Both may exhibit leaves with spinose teeth. The stigmatic surfaces are similar, that is, they are of the red oak type (4 under ERYTHROBALANUS in Table 1). The inner wall of the acorn shell is tomentose in each. Actually, the only distinction which holds between the two species is the position of the abortive ovules; these are basal in *Q. emoryi* and apical in *Q. agrifolia*. Can this feature, then, be considered as infallable for the ultimate segregation of *Quercus* species into the subgenera? Apparently not, for *Q. chrysolepis* Liebm. and *Q. tomentella* Engel., which are conceded by taxonomists to be red oaks, show basal abortive ovules. For what reason is *Q. emoryi* classified as a white oak; why *Q. agrifolia* as a red oak? On what basic standards have *Q. chrysolepis* and *Q. tomentella* been classified? The answer is obviously debatable, as is indicated by conflicting expressions of opinion in modern references. Trelease, for example, lists *Q. emoryi* as a red oak in contrast to all other authors, and places *Q. chrysolepis* and *Q. tomentella* in a third subgenus, PROTOBALANUS, a division which has not found favor with other systematists (24). Sargent, in his Silva (19) and Manual (20) reverses the position of the latter two species, apparently basing his decision upon similar data.

TABLE 1

Features characterizing Erythrobalanus and Leucobalanus as interpreted at present

ERYTHROBALANUS	LEUCOBALANUS
1—Acorns mature in two years.	1—Acorns mature in one year.
2—Inner surface of acorn shell tomentose.	2—Inner surface of acorn shell glabrous.
3—Leaves or their lobes bristle-tipped, or with spiny teeth.	3—Leaves or their lobes neither bristle-tipped, nor with spiny teeth.
4—Styles elongated, finally recurved; stigmatic surfaces gradually dilated.	4—Styles short; stigmatic surfaces abruptly expanded.
5—Abortive ovules apical.	5—Abortive ovules basal.

It is admitted that these exceptions to the rules upon which the subgenera are based are few in number. Nevertheless, they are exceptions, and for this very reason seriously hamper the effectiveness of this classification. Illustrating as they do the lack of infallible criteria for assigning species to one or the other subgenus, their anomalous position points to an important flaw in the present classification, particularly if this is to indicate natural affinities.

THE RÔLE OF WOOD ANATOMY IN CLASSIFICATION

As stated previously, it has become increasingly evident that some of the data accumulated in the comparative anatomical study of the *Quercus* species could be used to advantage in clarifying the confusion now existing within the genus, particularly as regards the precise limits of ERYTHRO- and LEUCOBALANUS. The interpretation of anatomical data as an aid in solving difficult taxonomic problems is relatively new, but this tool has already proven of undisputed value, which justifies its introduction into the present discussion (9, 11, 15, 23, 25, 27).

Systematists will be forced to go beyond the traditional use of floral organs and their derivative parts (fruits, seeds, etc.), if natural relationships and phylogenetic trends are to be clearly established among plants. In assaying the importance of the above-mentioned features to their full value, overemphasis has resulted, and many unjustified taxonomic problems have arisen as a result. The persistent use of acorn maturation in defining the red and white oak groups illustrates this point. If further progress is to be made, data compiled by the taxonomist, the anatomist, the cytologist, the geologist, the geneticist, etc., must all be correlated and the information weighted according to the particular problem.

Leading taxonomists are already committed to the idea that anatomy serves as an accurate guide in defining the limits of the larger natural units of vegetation, that is, the family, the genus, and in this instance, the subgenus. Differences between species are less prone to be as significant as the above, and usually are the result of insufficient sampling. There is no indication that external differences between closely related species necessarily imply internal differences. This does not mean that differences never occur between species, but if these are present, exceptional care must be exercised to test adequately their validity. It is imperative that in the continued acceptance of wood anatomy as a taxonomic tool, negative evidence be as clearly exposed and weighed as positive evidence. If high standards are to be demanded of the systematist, equally high standards must be met by the applied botanist.

EVIDENCE OF SUBGENERIC LIMITS PRESENTED BY ANATOMICAL DATA

Oak wood as a type is easily recognized. The sapwood is creamy white to buff; the heartwood varies from light tan to dark brown, with or without a reddish cast. The wood ranges from typically ring porous to semi-ring porous, that is, with either an abrupt or gradual transition in size from the larger springwood vessels, arranged in a one to several-seriate zone, to the small summerwood pores (Figs. 1–4). The latter are radially aligned and

embedded in flame-shaped tracts of tissue, which, to the naked eye, appear light in color. At higher magnifications, this tissue is resolved into a mass of longitudinal parenchyma and vasicentric tracheids, similar in all respects to that sheathing the springwood vessels (Figs. 3, 4). The transverse section is further figured by concentric bands or metatracheal-zonate bands of parenchyma,[2] which at 10×, appear as fine white lines extending tan-

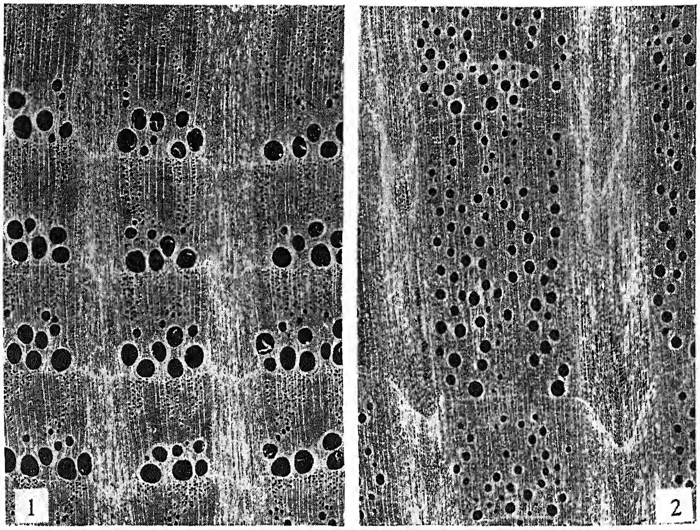

Fig. 1. *Q. bicolor* Willd. (9×) Illustrating the true ring porous type of oak wood. Note also the characteristic appearance of the thin-walled, angled summerwood pores of white oaks at low magnifications.

Fig. 2. *Q. virginiana geminata* Sarg. (9×) Illustrating the semi-ring porous type of oak wood common among the live oaks. Note the appearance of the thick-walled, rounded summerwood pores of the red oaks at low magnifications.

gentially throughout the summerwood. The wood rays are of two types, *a*, simple and uniseriate, and *b*, compound or aggregate and multiseriate (Figs. 5, 6). The multiseriate rays strikingly figure the various planes of section and are the most characteristic feature of oak wood. On the transverse section, as viewed with the naked eye, they are visible as more or less widely spaced, broad, light bands which stand out against the darker background of fibrous tissue; slight magnification reveals that the large rays are separated by numerous fine white lines, the uniseriate rays. In flat-sawn lumber, the large rays are staggered and vary in length along the grain from one-sixteenth to several inches. Quarter-sawn boards exhibit

[2] Short strands of longitudinal parenchyma more or less united tangentially into zones whose course runs irrespective of the pores.

conspicuous, extremely high ray flecks which are fairly widely spaced and form a figure not duplicated in any other native wood.

With special reference to the present problem of determining subgeneric limits, it has long been known that there are two sharply defined groups in the genus *Quercus*, distinct from one another on the basis of variations in the structure of the secondary xylem (1, 3, 16). Anatomists have recognized the close parallelism of these two groups to LEUCOBALANUS and

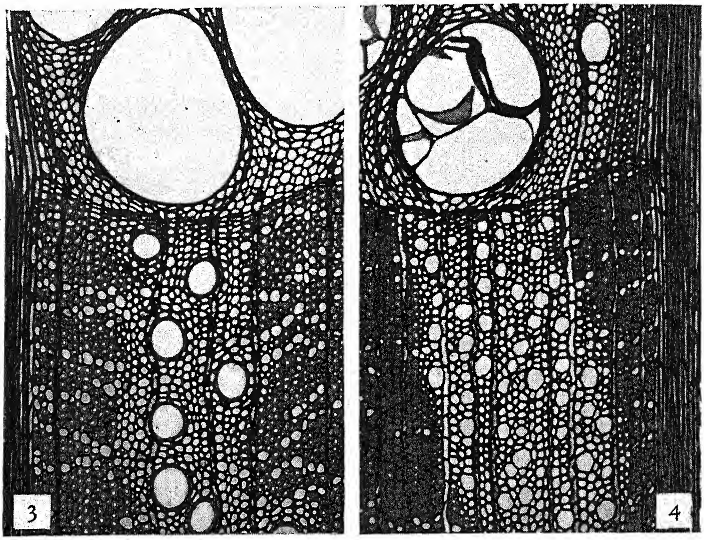

Fig. 3. *Q. coccinea* Muench. (60×) Showing the rounded, thick-walled summerwood pores of the red oaks at higher magnification. Note the absence of tyloses from the springwood vessels.

Fig. 4. *Q. alba* L. (60×) Showing the thin-walled, angled summerwood pores of the white oaks. Note the tyloses in the springwood pores.

ERYTHROBALANUS of systematic botanists, even though the latter have never used these features. The important rôle they play has now become apparent.

The structural and physical features of the wood of the anatomical subdivision of *Quercus* are tabulated below.

TABLE 2

Structural and physical characteristics of red and white oak wood

RED OAK TYPE CORRESPONDING TO ERYTHROBALANUS	WHITE OAK TYPE CORRESPONDING TO LEUCOBALANUS
1—Heartwood with reddish cast	1—Heartwood light tan to brown
2—Tyloses sparse in heartwood	2—Tylose abundant in heartwood
3—Summerwood pores rounded, thick-walled (3 to 8 microns, Figure 3)	3—Summerwood pores angled, thin-walled (less than 3 microns, Figure 4)

The first two of these overlap and can not be used with certainty. The third is apparently absolute. It seems reasonable to assume that this indication of group relationships is of equal or greater importance as compared to that signified by those features which have been utilized in the past (see Table 1), especially in view of the contradictory nature of these latter-mentioned criteria. This assumption gathers further strength from an analysis of the data covered in the succeeding paragraphs.

The division of *Quercus* species on the basis of wood anatomy closely conforms to that evolved from the criteria listed in Table 1, When the present study was initiated, no exceptions to this rule were known, or if known, had escaped critical attention. As the list of species studied has grown, however, so has the list of exceptions, until at the present time, after a comprehensive examination of some fifty "species" and "varieties", eight have been found, which, on the basis of this criterion (3 in Table 2), are at variance with the groupings accepted by taxonomists. Of extreme interest is the fact that all of these are placed by systematists in LEUCOBALANUS, no departures occurring among the red oaks. Furthermore, these are the only exceptions to the general rule that the white oaks should possess leaves devoid of bristle-tipped lobes or spiny teeth on the leaf margins. The "white oaks" exhibiting "red oak" wood are *Q. emoryi* Torr., *Q. dumosa* Nutt., *Q. virginiana* Mill., *Q. reticulata* H. B. K., *Q. arizonica* Sarg., *Q. oblongifolia* Torr., *Q. engelmanni* Greene, and *Q. douglasii* Hook. & Arn.

Considering now the problem of devising a classification permitting of the absolute segregation of *Quercus* species into red and white oak types, a means of separation must be found that will retain the natural units and at the same time permit of no exceptions to the rule. As little change as possible should be made in the existing classification in order to avoid confusion upon the adoption of the revised system. Analysis of the correlation between wood anatomy and leaf-form reveals a plausible change which is at once simple and satisfies every demand made upon it by systematic botany. The proposal is made that the two groups, ERYTHROBALANUS and LEUCOBALANUS be retained, but that they be redefined as follows:

Leucobalanus:

Summerwood pores angled, thin-walled; leaves devoid of spinose teeth or bristle-tipped lobes.[3]

Erythrobalanus:

Summerwood pores rounded, thick-walled; leaves wholly or in part with bristle-tipped lobes, apex apiculate, or margins with spiny teeth.

[3] Leaves may be coarsely sinuate-toothed, as in the "chestnut oaks," but the ends of the teeth are rounded, not spiny.

The value of the above definitions is at once evident, since they clearly define the natural groups, and are usable in the field and herbarium by expert and layman alike. Their adoption affects the position of the eight species listed above, and these only; these species should be transferred from LEUCOBALANUS to ERYTHROBALANUS.

It may be argued that the genus *Quercus* can be subdivided arbitrarily by the use of existing criteria without employing a new variable, wood anatomy. A distinct subdivision of species might be suggested based on any one feature listed in Table 1. Were only an artificial segregation of species the ultimate objective, this possibility is granted. If the principles of taxonomy are to be respected, however, a grouping, to be acceptable, must indicate the natural affinities that exist between species. The corollary follows, therefore, that the measure of such subdivisions must be indicative of these relationships, and it is obvious from the previous discussion that the features listed in Table 1 are inadequate for such a purpose. Further, if the subdivisions are to be workable, the basic criteria must always be present. Leaves and wood are invariably available for examination, both in the forest and in the herbarium, in the latter because it is customary to mount sprays of foliage on herbarium sheets, thus supplying sufficient wood (the twig) and leaves to permit of accurate diagnosis. This obviates the difficulties encountered in classification when only sterile material is available. No features exhibited by the oaks, other than those proposed, display such a positive correlation and are so easily recognized. None have such omnipresence. There are no exceptions to the rule.

THE EVIDENCE AGAINST ADDITIONAL SUGBENERA

This discussion cannot logically be concluded without considering the possibility of the creation of a third subgenus, this to include those controversial species which inherently present composite features present in both the red and white oaks. Critical examination of the eight species it is proposed to transfer from LEUCOBALANUS to ERYTHROBALANUS reveals that all have evergreen foliage (persistent until the second season) with the exception of *Q. douglasii*. The interpretation of the characteristic of persistent foliage is, in itself, intangible, but greater weight may be assigned to this feature when it is considered in conjunction with the fact that all of the evergreen oaks have wood of the red oak type. Thus, within the new boundaries of ERYTHROBALANUS proposed in this paper, there are fourteen species[4] which exhibit evergreen foliage. The question arises, there-

[4] *Q. emoryi* Torr., *Q. dumosa* Nutt., *Q. virginiana* Mill., *Q. arizonica* Sarg., *Q. reticulata* H. B. K., *Q. oblongifolia* Torr., *Q. engelmanni* Greene, *Q. agrifolia* Nee, *Q. vaccinifolia* Kell., *Q. wislizenii* A.DC., *Q. hypoleuca* Engel., *Q. myrtifolia* Willd., *Q. chrysolepis* Liebm., *Q. tomentella* Engel.

fore, as to whether or not this group is sufficiently distinct to warrant subgeneric rank.

The red and white oaks have been defined through the correlation that exists between leaf-form and specific features present in the summerwood. The other features now in common use diagnostically have been shown to be unsatisfactory, since they fail to denote accurately the natural affinities occurring in the genus. A third subgenus, were it to be assigned equal rank to LEUCOBALANUS and ERYTHROBALANUS, must show a similar correlation between leaf-form and wood anatomy. Furthermore, both leaf-form and wood structure, as exhibited by this third group, would have to be sufficiently different in character from those of the other groups to permit of ready recognition.

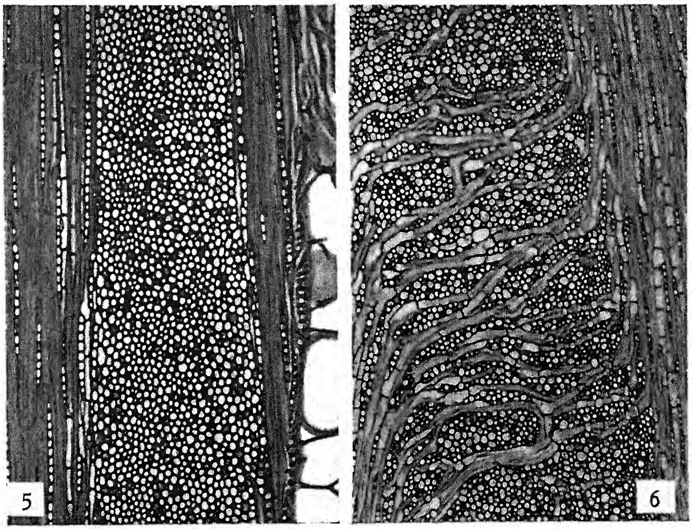

Fig. 5. *Q. stellata* Wang. (60×) Illustrating the true compound ray common to all oaks. Note the uniseriate rays.

Fig. 6. *Q. virginiana* Mill. (45×) Illustrating the aggregate ray type common only among the live oaks.

In leaf features alone, the evergreen oaks are certainly distinct. However, in attempting to correlate the anatomy of the wood with evergreen habit, sufficient variation is encountered to cast doubt upon the merit of this feature in assigning subgeneric rank. As a group, the species enumerated on this page tend to possess wood of the semi-ring porous type, in contrast to the ring porous condition present in the deciduous forms (Figs. 1–4); nevertheless, *Q. emoryi*, *Q. arizonica*, and *Q. myrtifolia* commonly possess ring porous wood. The tendency to form aggregate rays in

lieu of those of the compound type is found only in certain of these species. Scalariform perforation plates, an extremely rare feature of oak wood, are restricted to this group, yet this feature cannot be used, due both to the infrequency of its occurrence and to the fact that is evinced by but several of the species listed. Sclerosed tyloses are also present, but too sporadic to be significant. Springwood vessel diameters,[5] on the average, are smaller in these species than in the deciduous forms, but certain species in each group overlap sufficiently to nullify the mathematical significance of this character.

Within ERYTHROBALANUS the evergreen oaks form a small congeries which is so well defined that it cannot be ignored. This situation is not denied; nevertheless, these species, considered together, should not be accorded subgeneric rank on the basis of present evidence. Perhaps, with additional study, the group will attain greater distinctness as an entity. It is admitted that the evergreen oaks have many characters in common, and since they exhibit all of the xylary features accepted as primitive for the oaks (as well as certain other plant groups)[6] they deserve a significant niche in the phylogeny of the genus. The premise seems logical to designate this group as the "live oak" type within the subgenus ERYTHROBALANUS.

Comparable arguments may be advanced that no other aggregate of species within the newly defined LEUCO- and ERTHROBALANUS merits subgeneric rank, however distinct it may be on the basis of foliage alone. The so-called "chestnut oaks", admitted to be a definite segregate of LEUCOBALANUS, have anatomical features identical with the other white oaks. The Rubrae and Laurifoliae of Small (21) merge insensibly on the basis of wood anatomy. Nor do the Virginae of Small have any significance when the above mentioned facts are considered. Small's Albae are merely a southeastern extension of LEUCOBALANUS. For field identification Small's divisions may have intrinsic value, but as indicators of natural affinities they cannot be accepted.

In conclusion, it is conceded that the changes suggested in the classification of the oaks are tentative, pending such time when all the species embraced by LEUCOBALANUS and ERYTHROBALANUS can be critically examined. Certainly, wood anatomy promises to be a valuable tool in clarifying the confusion now prevailing in this genus. Further investigations are under way to determine whether variations in the anatomy of the secondary phloem will prove equally valuable in classification, and

[5] The tangential diameter of the pores is commonly used, as this is a more conservative measure than the radial axis.

[6] Tendency toward diffuse porous wood and aggregate rays, and scalariform perforation plates in the smaller summerwood vessels (2. 7 10, 23, 26).

whether these data will substantiate the deductions made in this paper on the basis of wood anatomy. Preliminary study has indicated that such will be the case; these results will be reported at a later date.

SUMMARY

The criteria used at present in delimiting LEUCOBALANUS and ERYTHROBALANUS in the genus *Quercus* do not provide for a satisfactory segregation of species according to their natural affinities.

Such flagrant exceptions occur that the logic of these criteria is questionable. No one feature now in common use in defining either of the two subgenera is not duplicated in the alternate subgenus.

Two types of wood structure are shown to exist within the genus *Quercus*, permitting of an absolute segregation of species.

The two groups defined on the basis of wood anatomy closely parallel LEUCOBALANUS and ERYTHROBALANUS as now recognized by systematists, with the exception of the following species: *Q. emoryi* Torr., *Q. dumosa* Nutt., *Q. virginiana* Mill., *Q. reticulata* H. B. K., *Q. arizonica* Sarg., *Q. oblongifolia* Torr., *Q. engelmanni* Greene, *Q. douglasii* Hook. & Arn.

The eight species listed above are the only exceptions to the rule that the leaves of the white oaks be devoid of bristle-tipped lobes or spiny teeth on the leaf margins.

An absolute correlation exists between leaf-form and the structure of the summerwood; those species having leaves, either wholly or in part, with bristle-tipped lobes or spiny teeth, all possess wood of the red oak type.

LEUCOBALANUS and ERYTHROBALANUS are redefined on the basis of this correlation. Pursuant to this new definition, the eight species listed above are transferred from LEUCOBALANUS to ERYTHROBALANUS.

All of the evergreen oaks have wood of the red oak type, and the feasibility of creating a third subgenus to include these species is indicated. The evidence being to the contrary, it is proposed to designate these species as the "live oak" type in ERYTHROBALANUS.

The wood of the evergreen oaks alone exhibits all of the anatomical features conceded as primitive for the oaks, namely, tendency toward semi-ring porous wood and aggregate rays, and scalariform perforation plates in the smaller summerwood vessels. These features are sporadic, however, and no one is common to all live oaks. There is no absolute correlation possible between evergreen habit and wood anatomy other than that stated above.

No subgroups within LEUCOBALANUS or ERYTHROBALANUS, as defined in this paper, merits subgeneric rank, however distinct in foliage.

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Pocomoke Swamp: A Study of a Cypress Swamp on the Eastern Shore of Maryland

George Francis Beaven and Henry J. Oosting

(with five figures)

Introduction

Though the Pocomoke River Swamp greatly resembles the Dismal Swamp in physical characteristics, little attention has been given it. The latter is usually regarded as the most northern of the extensive southern cypress swamps characteristic of the Atlantic Coastal Plain. Separated from the Dismal Swamp by Chesapeake Bay, the Pocomoke Swamp appears to be an isolated northern extension of the larger development on the mainland and offers an excellent opportunity for comparative study.

The swamp and its relation to the surrounding territory

Once considered an almost impenetrable wilderness, the swamp was early exploited for its valuable timber. Consequently it has been lumbered over its entire extent. Much of its original area in the upper part is now drained and cultivated. However, because of the low elevation, parts of the swamp have not been drained and have seldom been entered since lumbering ceased many years ago. These areas, mostly along the tidal part of the river, are undoubtedly much like the original forest.

Pocomoke River, a tributary of Chesapeake Bay, has its source in lower Delaware, flows southward through southeastern Maryland and empties into Pocomoke Sound. The swamp at present occupies a narrow strip along each bank of the river and its tributaries. It is about 30 miles in length and varies from less than 0.5 to nearly 2 miles in width. The lower part of the river is brackish and is bordered with salt marsh which extends several miles upstream to where the swamp begins, about opposite the village of Rehobeth in Somerset County. Above Rehobeth the wooded swamp is continuous except where wide bends in the river bring it to the margin of the flood plain bordered by low, pine-wooded bluffs.

The only extensive areas of fresh water marsh occur at the mouth of Nassawango Creek and on a few river bends near Snow Hill. Otherwise emergent aquatics occur only as an extremely narrow strip along the river and mainly in its upper reaches. The portions of the swamp adjacent to the river are regularly flooded and drained by the tide which affects most of the river to above Snow Hill. Its average rise and fall is about 2.8 feet at Pocomoke City and 3 feet at Snow Hill. A few hundred yards from the river drainage at low tide is less complete and there is some standing water at all times. Even where ditches have been dug, the level contour, fallen

logs, cypress knees and accumulation of plant debris prevent much run-off at low tide. The land rises very gradually from the river and as it reaches an elevation above high tide it becomes less swampy with a gradual transition from swamp to upland forest. Occasionally there are more abrupt rises and the boundary of the swamp is then well marked.

The upper part of the river above the reach of the tide and in the neighborhood of the Maryland-Delaware line apparently was once bordered by a swamp of much larger extent than the narrow belt along the tidal portion of the stream. This region, however, has been more extensively lumbered and has been largely drained by deepening the channel of the river and by extensive ditching. Much of it is now in cultivation and possesses a characteristic black colored soil noticeable in the vicinity of Gumboro, Delaware. The original poor drainage resulted in an accumulation of peat of some depth. As a result of drainage, cutting and a severe drought in 1931, forest fire swept the whole area and burned persistently for about six months, locally destroying most of the peat accumulation and all the remaining forest. The conflagration was worst in an area now known as the Burned Swamp. Here the burning of the peat lowered the ground level so that an extensive area became covered with shallow water in spite of the drainage ditches. These have recently been deepened and much of the area at first covered with water is now dry causing consequent readjustments in the flora. There appear to be no cypress trees left in this vicinity and at present no trees of any kind grow along the most severe part of the burn. The parts where water is still standing are in the beginning of a hydrarch succession which should progress rapidly unless further disturbed by drainage.

The climate of the region is typically oceanic because of the ocean to the East and Chesapeake Bay to the West. Climatic data (Weeks, 1932) covering 21 to 26 years of record give for Pocomoke City a mean annual temperature of 57.3° F. July is the warmest month with a mean of 77.8° and February is the coldest with a mean of 36.6°. The average date of last killing frost in spring is April 14, and that of the first in the fall is October 29 giving a growing season of 198 days. Rainfall is well distributed throughout the year, being slightly greater during the growing season than in the winter, and averages 39.12 inches annually. Snowfall is light and seldom remains long on the ground, the average annual fall being 11 inches. The climatic conditions of the Dismal Swamp are very similar although, being to the south and on the mainland, the temperatures there are consistently a few degrees higher, the annual precipitation is several inches greater, and the growing period slightly longer (Kearney, 1901).

Worcester County, where most of the study was made, lies wholly within the coastal plain as does almost the entire peninsula, and is the only county in Maryland bordering on the Ocean. Its elevation varies from sea level to 51 feet above and averages about 35 feet (Perkins and Bacon, 1928). The total fall of Pocomoke River throughout the length of the county is slightly more than 30 feet which accounts for its sluggish flow and the presence of the swampy areas along it.

The soils have developed from gravel, sand, silt and clay transported by the Delaware, Susquehanna and Potomac Rivers from the Allegheny Ridges and deposited in coastal waters. They are mostly sandy loams or silt loams, porous enough to be well drained in spite of the low elevation (Perkins and Bacon, 1928). Soil in the swamp has no definite texture and if drained would be classified as muck or Portsmouth loam. The muck is usually underlain with the characteristic sandy subsoil of the region.

THE FLORA AND ITS ECOLOGICAL RELATIONSHIPS

Though climatic and physiographic conditions are much the same for all the region there are yet a number of varying factors, particularly edaphic, which limit certain species and communities to restricted areas. Saturated soil, alternate flooding and draining, standing water, accumulated organic material in varying quantities, sandy ridges, all contribute to the diversity of vegetation. Saturated soil and standing water are unfavorable to most plants because of poor aeration and an acid condition due to the accumulation of carbon dioxide (Kurz, 1928) and it has been shown by Bergman (1920) and others that under these conditions poor root growth results. Plants surviving must consequently have adaptations permitting root respiration or else, with limited root systems, be equipped with structures which maintain a slow rate of transpiration. The necessity for special leaf, stem or root modifications to meet the varying requirements of habitat limits the number of species appearing in any one place. The extensive literature on bog and swamp habitats treats these factors as well as wave action, ice, temperature and humidity, light and effects of drainage with varying degrees of emphasis (Rigg, 1916). Most of these factors are acting in the Pocomoke Swamp but, as elsewhere, not all are of equal importance in the distribution of the vegetation. The associations which occur must be explained by local conditions peculiar to this swamp and, although often overlapping and possessing many species in common, certain divisions on the basis of moisture and light conditions can be recognized. Communities which may be termed *Swamp Forest*, *Forest Stream Border*, *Fresh Water Marsh*, *Upland Border*, and

Burned Area will be discussed separately and in some cases further subdivisions made.

The nomenclature used for flowering plants is essentially that of Gray's Manual (seventh edition). The pteridophytes follow Bomquist (1934).

SWAMP FOREST

The swamp forest occupies the bulk of the area studied. Other communities discussed are, with the exception of the Burned Swamp, more or less marginal and of limited extent. The swamp is densely and evenly forested with a closed canopy producing heavy shade. Herbs and shrubs on the forest floor are limited in number. The soil is normally very wet or covered with shallow water in which sphagnum is abundant. The forested swamp might be divided into a tidal zone which is regularly inundated and drained, and a non-tidal zone, adjacent to the upland, with shallow water areas unaffected by the tide. However, with few exceptions the vegetation is uniform throughout and seems best regarded as a single community.

Trees

Cypress (*Taxodium distichum*) and swamp black gum (*Nyssa biflora*) are the dominant trees. They are mostly second growth with the exception of a few gnarled and misshapen specimens. In a typical stand the cypress ran from 13 to 24 inches in diameter breast high but were rather uniformly 80 years of age. Red maple (*Acer rubrum*) is equally abundant but occurs only infrequently in the dominant stratum. *Nyssa sylvatica* is a common associate and occasionally large specimens of sweet gum (*Liquidambar styraciflua*) are found near the upland border. Green ash (*Fraxinus pennsylvanica* var. *lanceolata*) is common throughout the swamp but is never very large. Small specimens of swamp cottonwood (*Populus heterophylla*) are occasionally noted. Within the swamp on slightly elevated ground are isolated specimens of loblolly pine (*Pinus taeda*) and pond pine (*Pinus serotina*), the latter being more abundant where standing water or poor drainage render the habitat more acid.

White cedar (*Chamaecyparis thyoides*) is scarce near the river but in the non-tidal portions of the swamp near the upland border it may become fairly abundant and form nearly pure stands. Such a tendency is noted throughout its range and in Virginia and North Carolina (Korstian and Brush, 1931) pure glades of white cedar have been found to occupy very acid soil and shallow peat underlain by sand. In Pocomoke Swamp the non-tidal portion with its standing water is more favorable to the formation of peat with its accompanying high acidity, and, where the white

cedar is most plentiful, the spongy peat accumulation has built up the soil level so that there is usually very little standing water. This condition seems more favorable to the establishment of white cedar than does the presence of deeper water.

Cypress is most abundant near the river's edge but seldom forms extensive pure stands except in shallow mill ponds on tributary streams (fig. 1) where the raising of the water level has excluded other species. Only a short distance from the river cypress decreases and black gum becomes increasingly more abundant so that over wide areas it is the most

Fig. 1. Open cypress stand in ponded stream. Note immense relic stump at left.

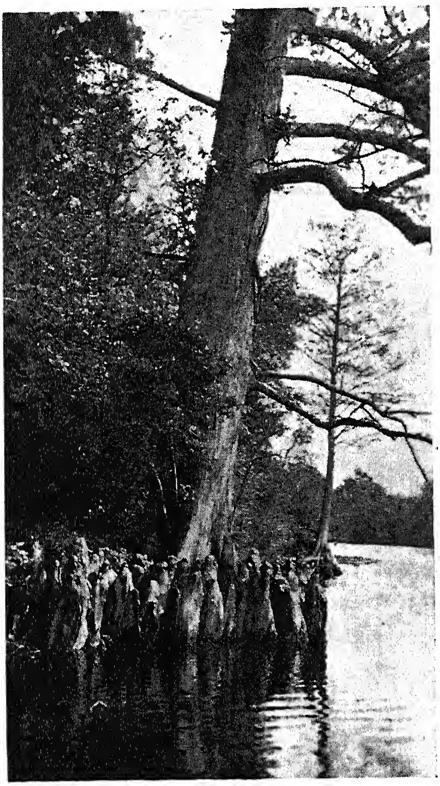
important tree. Especially where the water level may rise highest among the trees, the cypress, and to a lesser extent the gum, show characteristic swollen bases. Cypress knees are well developed and numerous, usually ranging up to about 2 feet in height. Since this is the depth of average tidal flooding it conforms with the contention of Kurz and Demaree (1934) that knees grow only to the level of average high water. In well-drained soil they are never present. At the river shore these knees form almost solid walls around the trunks next to the stream (fig. 2).

A frequent understory tree is the sweet bay (*Magnolia virginiana*), which is everywhere abundant in the swamp. Specimens of holly (*Ilex opaca*) and red cedar (*Juniperus virginiana*) are scattered throughout but are more abundant where the soil is least saturated. The margins of small streams and the river shore support numerous specimens of fringe tree

(*Chionanthus virginica*), blue beech (*Carpinus carolinana*), black alder (*Alnus rugosa*), and many viburnums of nearly tree size.

Vines

Many lianas drape the trees and occasionally reach their tops. Most noticeable are *Vitis* spp., *Bignonia capreolata*, *Smilax laurifolia*, *S. Walteri*,



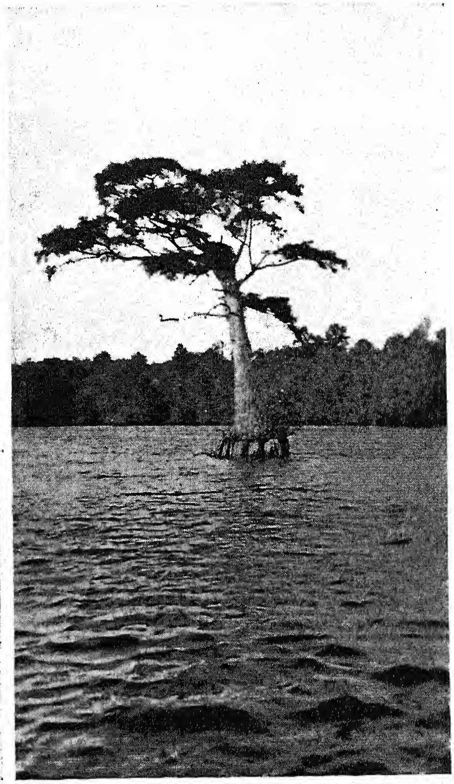


Fig. 2. Typical stream-margin habit of cypress with knees closely clustered at base.

Fig. 3. Isolated cypress characteristic of shallows in the river.

Tecoma radicans, *Rhus toxicodendron*, *Psedera quinquefolia*, and *Lonicera japonica*. *Bignonia capreolata* and *Smilax laurifolia*, both evergreen, are here near their northern limit, as is the muscadine grape (*Vitis rotundifolia*). Also occasionally found on trees are two interesting plants of southern range, the epiphytic gray polypody (*Polypodium polypodioides*) growing high on limbs of black gum and the parasitic mistletoe (*Phorandendron flavescens*) usually found on limbs of gum and maple. *Dioscorea glauca*,

Apios tuberosa, and *Mikania scandens* often overrun the lower bushes which may also be infested with love vine (*Cuscuta compacta*).

Shrubs

The shrubby growth, while not profuse or rich in species, contributes much to the beauty of the swamp. Although ranging through all parts, most species are more abundant in places where the shade is least dense and some, such as the viburnums, are mostly present near the swamp border along open streams. Ericaceous shrubs are plentiful and include *Rhododendron nudiflorum*, *Leucothoë racemosa* and several species of vaccinium, producing their flowers in early spring, while *Rhododendron viscosum*, *Lyonia ligustrina* and *Clethra alnifolia* blossom in the summer. Numerous and conspicuous in late spring and early summer are *Viburnum dentatum*, *V. nudum*, *V. cassinoides*, *V. prunifolium*, *Cornus amomum* and *Itea virginica*. *Decodon verticillatus* and *Cephalanthus occidentalis* flower in late summer, the former being common throughout the swamp forest. Not as numerous, but noticeable in fall and winter with their bright red fruits, are *Ilex verticillata*, *Pyrus arbutifolia*, *Benzoin aestivale* and *Evonymus americanus*. Occasionally along the river and very abundant near its mouth are large bushes of *Baccharis halimifolia*.

Herbs

Where the tide periodically floods the ground, especially in the dense shade of the forest, the number of species of herbaceous plants is not large. Very noticeable, however, are the ferns, *Osmunda cinnamomea*, *O. regalis* and *Lorinseria areolata* being most frequent. *Glyceria obtusa*, *Carex intumescens*, *C. lupulina*, and *C. folliculata* grow in scattered clumps, the extensive areas between being thinly populated with *Polygonum hydropiperoides*. *Polygonum arifolium* and *P. sagittatum* sometimes grow here in tangled masses. Other conspicuous herbs are *Impatiens biflora*, *Thalictrum polygamum*, *Rudbeckia laciniata*, *Bidens comosa*, *B. discoides* and several species of *Aster*.

Deeper in the swamp, where the tide has little effect and the water seldom is of much depth, are a wider variety of herbs. Those mentioned above are present, with the addition of clumps of *Carex debilis*, *C. crinita*, *C. serosa*, *Cinna arundinacea*, *Leersea virginica*, and *Rynchospora corniculata*. Covering the mud between these, the lizard's tail (*Saururus cernuus*) is by far the most abundant herb. Usually as isolated specimens and widely scattered, are *Boehmeria cylindrica*, *Ludvigia alternifolia*, *Lycopus rubellus*, *Eclipta alba* and the attractively flowered *Gentiana latifolia*, *Chelone glabra* and *Asclepias incarnata* var. *pulchra*. Throughout the entire

swamp forest are scattered, though frequent, specimens of the umbellifer, *Oxypolis rigidior* var. *longifolia.*

Rarely, near where bog iron ore was dug, are found small pools of deeper water in which grow *Potamogeton pulcher* and *Peltandra virginica.* Decayed stumps, logs and raised tussocks in this area are usually covered with *Mitchella repens*, *Trillium sessile*, *Anemone quinquefolia*, *Viola cucullata*, *Habenaria clavellata*, *H. cristata* and the fern *Athyrium acrostichoides.*

FOREST STREAM BORDER

Throughout most of the length of the river there is no marsh between the swamp and the water, and this is likewise true of all the tributary streams except in a few small areas at the mouths of some of them. This is probably accounted for by the strong tidal movement in most cases, and the narrow, deep channels with the consequent lack of sedimentation providing no new areas for invasion by marsh plants. The swamp forest represents an edaphic climax which has replaced most marsh land and has now become quite stable. The cypress trees extend to the water's edge (fig. 2) and, at rare places where there are shoals, may be found some distance out in the river (fig. 3). Hence most of the species characteristic of the tidal swamp forest are present along the stream borders, but there are a number much more abundant here than further in, and some additional ones make their appearance.

Extending a short distance out from the shore to the channel is a gently sloping shallow area of soft mud which is partly exposed at extreme low tide. From near Pocomoke City to Snow Hill, and probably as far as tide water reaches up the river, this strip is marked by a narrow zone of *Nymphaea advena*, growing from near the bank to just beyond the low tide mark. Nymphaea disappears below Pocomoke City, probably due to slight salinity at high tide in dry seasons.

It is interesing to note here the resistance of cypress to this occasional salinity. During an unusually dry season in the fall of 1930 the river water at Pocomoke City had a distinctly salty taste and fish characteristic of salt water were caught from the bridge there. *Nymphaea advena* showed considerable injury at this time, as did also a number of other plants at the water's edge, but the cypress showed no ill effects. Tides lower than usual prevented the salt water penetrating back into the swamp but some cypress were completely surrounded by it for several weeks. Some distance below the point where salt marsh appears there are a few old cypress trees near Cedar Hall growing at the river's edge but along a bank rising some distance above the water so that seepage of fresh water from the shore may explain their ability to survive there.

Orontium aquaticum and *Pontederia cordata* are often found next to the shore, within the zone of *Nymphaea advena*. Where the bank is slightly higher but still swampy, *Cicuta maculata*, *Sium cicutaefolium*, *Lobelia cardinalis*, *Aster* spp., and *Iris versicolor* are rarely present in addition to some species already mentioned in the swamp forest flora. On sandy spots, just at the high water mark, *Hydrocotyle umbellata* is sometimes found.

Species already named as members of the swamp forest but found in greater abundance overhanging the banks of streams are fringe tree, blue beech, black alder and rarely black willow (*Salix nigra*). Nearly all the shrubs of the swamp are in greater abundance here, *Viburnum* spp., *Vaccinium* spp., and *Rhododendron nudiflorum* all being conspicuous at flowering time. Also here the swamp rose (*Rosa carolina*) is noteworthy and in some places forms dense tangles. There is little of the herbaceous swamp flora present along the immediate margin of streams. Probably this is accounted for by water action and the lower soil level where the mud has been washed out between the trees and larger shrubs in a series of hollows all along the shore line. Vines are more in evidence as seen from the water for light conditions are far better than in the interior of the forest.

FRESH WATER MARSH

Areas which may be termed marsh are rarely present within the swamp limits. Along the lower part of the river, however, the swamp is entirely replaced by extensive areas of marsh. These might be classed as fresh, but contain numerous species characteristic of brackish water and many fresh water species are excluded. There is a gradual transition into salt marshes near the river's mouth. Since this marsh is so radically different and so sharply delimited from the swamp proper it will not be treated further here.

Only at the mouth of a few streams, locally in the upper river, and along tributaries, are there limited areas of fresh water marsh having a close relationship to the swamp. The soil in these marshy areas seems to have become recently available to emergent species. Apparently it was built up from silt deposited by the retarded current. A few marshy areas on tributaries of the river seem to have resulted from the draining of old ponds. These are partly invaded by shrubs and a few trees but changes in their outline and composition do not seem to be rapid.

Nearest the water, *Nymphaea advena* again forms the outer lines of vegetation and back of it *Pontederia cordata*, *Sagittaria latifolia*, *Peltandra virginica* and *Orontium aquaticum* are most abundant. Further within the marsh *Typha latifolia* is common and may form scattered dense stands. *Phragmites communis* is also found in pure stands at the mouth of Nas-

sawango Creek but is rare elsewhere. Other species are found scattered over the marsh in separate patches or are intermingled. Conspicuous among these are *Dulichium arundinaceum*, *Rynchospora macrostachya*, *Carex stipata*, *Trisetum pennsylvanicum*, *Elymus virginicus*, *Zizania aquatica* and occasional clumps of *Hibiscus* spp. Many species of carex, juncus and others of smaller stature are present, and where marsh merges with swamp the species named in the preceding section appear. Where shrubs enter the inner area, *Rosa carolina* and species of rubus are important. In the fall the marshes become bright with the blossoms of *Helenium autumnale*, *Bidens trichosperma*, *Aster paniculatus* and a few others. Although periodically flooded with the tide, the marshes are well drained at low tide and apparently differ little from those which do not border swamp land. Only in ponds beyond the influence of the tide is the deeper water sometimes covered with the floating leaves and blossoms of the water lily (*Castalia odorata*).

UPLAND BORDER

By upland border is meant the area of transition from swamp to upland and not the upland forest itself. The change may be abrupt or a gradual one with considerable mingling of species. This depends on whether the land rises abruptly or with very gentle slope and hence both narrow and broad transition zones may be found. The gradual change is usual where small lateral streams of short extent diverge and lose their identity, and the abrupt change is more often found along a stream where there is a narrow belt of swamp not intercepted by lateral branches. Also within the swamp are occasional raised sandy areas or islands which are not flooded with water and are quite dry at the surface though possessing a constantly high water table. These support a flora similar to that of the upland border.

Trees

The tendency of white cedar to become more abundant near the upland and sometimes form nearly pure stands has already been noted. This tree is characteristic of the transition zone but seems to do best just within the swamp where the forest floor has been built up above the water level by peat accumulation. Such a condition is more often found where the transition from swamp to upland is gradual. Along the upland border where the soil is less peaty are found a number of oaks, chiefly water oak (*Quercus nigra*), willow oak (*Q. phellos*), swamp chestnut oak (*Q. michauxii*) and white oak (*Q. alba*). Other broadleaved species, notably tulip poplar (*Liriodendron tulipifera*), river birch (*Betula nigra*) and beech (*Fagus grandifolia*) occur here, and at scattered points most species of the

upland forest may be found. Where the ground is mostly above swamp level, however, loblolly pine becomes the most abundant tree. In the upland it forms the extensive pine forests which are characteristic of this region and nearly everywhere surround the swamp. Virginia pine (*Pinus virginiana*) and short-leaf (*P. echinata*) are common only where the soil is definitely dry and sandy, although such areas may occur adjacent to the swamp on the more abrupt rises.

Shrubs

Probably the most notable characteristic of this transition zone is the abundance of evergreen shrubs which sometimes form dense thickets. Although numerous in individuals, the species are few and consist almost entirely of *Kalmia latifolia*, *Ilex glabra*, *Myrica cerifera*, and occasionally small trees of *Ilex opaca*. The first two frequently attain large size. On the ground are often found such small evergreens as *Mitchella repens*, *Gaultheria procumbens*, *Lycopodium complanatum*, and more rarely *Selaginella apoda*. Nearly all of these evergreens are also components of the upland forest but their greater abundance here must in some way be related to the presence of the swamp.

The most likely explanation of this preponderance of evergreen shrubs must lie in the fact that the lower levels of soil are permeated with the acid, oxygen-depleted swamp water. In this zone the underlying sandy layers are above the swamp level and the surface is not covered with the mud of the swamp, but is sandy and porous with little accumulation of peat. Although it is poorly drained because of the high water table, water normally never stands over it but sinks rapidly and drains off to the level of the swamp. Because of the slight elevation above the swamp, only a shallow surface layer of soil permits air to penetrate freely for the deeper layers remain saturated with water. This makes a habitat of very limited extent greatly resembling that described for the evergreen shrub bogs of North Carolina (Wells, 1932). The comparatively dry surface and fluctuating water table must exclude many swamp or marsh species. Other species are probably unable to develop a normal root growth since the oxygen deficiency of the soil water may render the habitat physiologically dry though possessing a high water table. Here the thick, waxy-coated leaf structure of the xerophytic evergreens should check transpiration and enable them to succeed much better than the thin leaved deciduous species whose usual widespread root development would be greatly retarded. Higher in the upland, the deciduous species with their rapid growth offer serious competition to the slowly growing evergreens. The lower winter temperatures in Maryland, and the isolation of this swamp

from those farther south, exclude from it the wealth of species found in the southern evergreen shrub bogs.

Although evergreen shrubs are most abundant, this border zone also contains scattered specimens of other shrubs characteristic of the swamp and a few which are more often found here than elsewhere. Of common occurrence are *Vaccinium* spp., *Rhus copallina*, *Amelanchier oblongifolia*, and where not too shaded, *Sambucus canadensis*. Several species of Smilax are abundant in places and with the thick growth of shrubs often make this border region more difficult to penetrate than any other part of the swamp.

Herbs

Where the upland border is densely shaded by trees and shrubs there are few herbaceous species. A scattering of those common to the swamp occur here and in addition *Arisaema triphyllum*, *Genetiana Saponaria*, rarely *Lilium superbum* and others less conspicuous may be found. *Asplenium platyneuron*, *Botrychium virginianum*, *Dryopteris intermedia*, *D. noveboracense*, *Athyrium asplenioides*, *A. thelypteroides* and, where quite dry, *Pteridium latiusculum* here offer a variety of ferns in addition to those of the swamp although none are plentiful except the last named, and that only in the drier parts.

The herbaceous vegetation of the more open parts of the upland swamp border is much more abundant both in individuals and species. This is especially true along roadsides entering the swamp. Only the characteristic plants will be mentioned. In rather wet semi-open situations are *Vernonia noveboracensis*, *Mimulus alatus*, *M. ringens*, *Gerardia purpurea*, *Ruellia ciliosa*, *Houstonia caerulea*, *Viola* spp. and many others. Less conspicuous are *Diodia virginiana*, *D. teres*, *Penthorum sedoides*, *Ludvigia palustris*, *Onoclea sensibilis*, *Dryopteris thelypteris*, *Eleocharis obtusa*, *Juncus setaceous*, *Rynchospora glomerata* and *Carex* spp.

BURNED AREA

The sections of the swamp that have already been described lie mostly along the length of the river and its larger tributaries in Worcester County. The upper part of the river near the southern border of Sussex County, Delaware, seems to have once been occupied by a swamp of considerable extent. This was somewhat different from that along the lower river in that it was entirely above tidewater and possessed a much deeper accumulation of peat. The timber and most of the peat have recently been destroyed by fire so that the region now is quite changed from its original condition and is undergoing successions which would justify further observation.

Due to the accumulation of peat, the fire which swept the area burned most persistently near the center of the swamp. At present this area has

Fig. 4. Burned swamp. Here the peat completely burned out and hydrarch succession was initiated.

Fig. 5. Lightly burned swamp. Secondary succession beginning with shrubs and sucker sprouts.

practically no accumulation of peat and the lower parts are covered in places with open water several feet deep (fig. 4). The bottom is hard and no plants have yet become established in the deepest spots although *Typha*

latifolia is present in clumps on the shallower areas and occasionally the Virginia chain fern (*Anchistea virginica*) and mermaid weed (*Proserpinaca palustris*) are present. On fallen logs and stumps *Rhexia virginica*, *Solidago fistulosa* and a few clumps of grass have at times obtained a temporary foothold.

Away from the center the water is shallower and here over a large area *Typha latifolia* has thoroughly established itself practically to the exclusion of any other species. Bordering this is an irregular region where the ground may be above the water level and again may be covered with standing water a foot or more in depth. Where the water is from a few inches to a foot deep *Anchistea virginica* and *Proserpinaca palustris* are usually the most abundant species although there are areas where *Typha latifolia* again forms dense stands. There are other herbaceous plants scattered in the deeper water but these are of more common occurrence in water only a few inches or less in depth. Conspicuously flowered herbs are *Rhexia virginica*, *R. aristosa*, *R. mariana*, *Mimulus ringens*, *Aster novi-belgii*, *Hypericum virginicum* and *Solidago tenuifolia*. In the same area *Scirpus pedicellatus* and *Juncus effusus* are both very abundant and commonly found are *Lorinseria areolata*, *Eleocharis tuberculosa*, *Juncus acuminatus*, *Carex lurida*, *Rynchospora microcephala*, *Ludvigia sphaerocarpa*, *L. alternifolia*, *Polygonum setaceum*, *P. pennsylvanicum*, *Pluchea foetida*, and cotton grass (*Eriophorum virginicum*). Bordering the water and especially along ditches by the roadside *Eupatorium purpureum*, *E. verbenaefolium*, *Vernonia noveboracensis*, *Erianthus saccharoides* and occasionally *Epilobium angustifolium* are conspicuous in late summer and fall. Sphagnum is here very abundant in shallow water along the margin and the dense mats of polytrichum on the marginal soil deserve mention. In wet soil near the borders of the water-covered areas are often found *Habenaria lacera*, *Spiranthes cernua*, *Xyris caroliniana*, and less frequently *Bartonia virginica*. On most of the raised areas of soil and especially along the roadside banks, *Spirea tomentosa* is the most abundant small shrub and with it as well as on stumps and tussocks *Solidago fistulosa* is conspicuous.

Bordering the area where fire destroyed all trees are extensive tracts where the peat has only occasionally burned to the subsoil and where a few scattered loblolly pines survived and are producing some seedlings. Here most of the water has been drained away. The ground is covered with sphagnum and polytrichum, while scattered everywhere *Juncus marginatus*, *Juncus effusus*, clumps of *Scirpus pedicellatus*, *Anchistea virginica*, and species of Ludvigia are the most abundant herbs. A shrubby growth is filling in the higher parts (fig. 5). Most common on these raised

areas are *Myrica cerifera*, *Itea virginica*, *Clethra alnifolia*, *Decodon verticillatus* and seedlings of red maple, sweet gum, loblolly pine, black gum, black willow and swamp cottonwood. Red maple seedlings are the most frequent of the forest tree species invading the area at present. Of smaller stature than these are species of Vaccinium and Rubus while beneath them *Lycopodium alopecuroides* is especially abundant.

PHYTOGEOGRAPHIC CONSIDERATIONS

Adams' (1902) suggestion that the present distribution of plants in the eastern half of the United States has resulted from a northward dispersal from the southeastern states since the recent era of glaciation has much evidence to support it. In the northern bogs many glacial marginal species have been retained as relicts of the time when the great ice sheet covered the northern United States and Canada (Dachnowski, 1911; Bird, 1923). Studies of wind borne pollen preserved in peat (Fuller, 1929; Sears, 1932), and the stratification of such peat deposits (Dachnowski, 1921) give evidence of climatic changes which occurred in the past. Since the great ice sheet receded there have probably been several major climatic fluctuations and evidence in general seems to indicate that for this region there is a trend to a warmer and drier period. The present distribution of bog and swamp plant societies (Transeau, 1903; Gates, 1911) indicates that the flora of bogs is a relict of past climatic conditions and in the south is being replaced by species characteristic of the present normal hydrophytic vegetation of swamps. If these facts are true, a comparison of the flora of Pocomoke Swamp to that of similar areas to the North and South might give some evidence of the extent here of this northward migration of southern species.

The tidal portions of the swamp forest are relatively stable and probably much like the original plant covering before the commencement of man's extensive lumbering activities. In the driest seasons the water level remains nearly the same and abnormally high tides caused by wind may still flood the innermost parts. Physical conditions have remained practically unchanged and fire has seldom entered. It is probable that selective lumbering of cypress and more recently of gum and other species has changed the proportion of valuable trees to inferior species but qualitatively it must be much the same. Most of the second growth is now rather old, showing the dominants, subdominants and understory growth of a mature community.

Upon comparison with other similar areas which have been described, this swamp, though possessing an acid soil and much sphagnum with

associated bog plants, still is quite different in dominant trees and associated species from the northern bogs of glaciated regions. However, it probably contains more plants which are of boreal relationship than does the pine forest of the South Atlantic coastal plain which surrounds it. Many of the species found here also occur in swamps much farther north and south, but those peculiar to bogs are mainly absent and the presence of *Taxodium distichum* and *Nyssa biflora*, as the dominant trees, gives an aspect like that of southern swamps. The region is largely cut off from the South and West by Chesapeake Bay and from the northern extension of the coastal plain by Delaware Bay. Though species common in the pine barrens occur on the raised sandy areas within the swamp, yet they do not form the characteristic associations of the barrens, and neither the New Jersey nor southern type of pine barren can be said to exist here. This has been explained as due not to climate but to the comparative immunity to fire which Chesapeake Bay with its many waterways intersecting the land has given the region (Lutz, 1934).

Most of the species collected in Pocomoke Swamp are also found in the Dismal Swamp (Kearney, 1901) and again many of the most common plants are also abundant in the Okefinokee Swamp of southern Georgia (Wright and Wright, 1932). The dominant trees, most abundant associates and understory plants are identical with those of the Dismal Swamp region as are also the zones along streams and the girdles of included open areas. Both lack an abundance of flowering plants in the densely shaded and flooded areas dominated by gum, cypress, and maple. It differs mainly from the Dismal Swamp in having fewer species of the evergreen shrubs developed so extensively in pocosins farther south. Most noticeable as common to the Dismal Swamp but absent from the Pocomoke Swamp are the growths of cane (*Arundinaria tecta*). This species has been collected in Maryland near Annapolis, considerably north of the Pocomoke region, but it has not been found in this swamp and probably has been prevented by Chesapeake Bay from migrating here.

From these generalizations it would seem that Pocomoke Swamp vegetation is more closely related to that of swamps farther south than to any vegetation northward. The dominants are largely southern species as are numerous conspicuous shrubs and herbs. The whole appearance is that of swamps much farther south but the presence of northern species leads to a question of just how numerous and important these may be.

In an attempt to show more clearly the relationships of the flora, the species collected have been distinguished on the basis of their ranges. Those species whose range lies largely to the north of the swamp are desig-

nated by N, and S indicates those which largely range southward. The ranges are admittedly generalized, having been determined largely from the available manuals. In general, those typically southern species which range north of the swamp but are restricted to the Coastal Plain have been considered as of southern affinity.

Obviously the numerous species of common occurrence from Canada to Florida have no bearing on the problem. These are unmarked. They comprise 57 per cent of the swamp flora (159 species). Of the species ranging largely northward there are 9, only 3.2 per cent of the total flora while 40 per cent or 111 species range largely southward. Of the 9 northern species, 7 are here near the southern limit of their ranges while only 36 per cent of the southern species here approach their northern limits. The swamp then provides conditions far more favorable to southern species and its flora is predominantly of southern affinity. The list of plants collected by Kearney in the Dismal Swamp area includes only one of the northern species (*Carex canescens*) found in Pocomoke Swamp and indicates a flora there far richer in southern species.

It seems then that the edaphic and climatic conditions of Pocomoke Swamp must be similar to those of swamps farther south. The oceanic climate, fluctuating tide, poor drainage and consequent poor aeration combine to restrict the flora and southern swamp species are best adapted to the extremes of this complex which requires special means of transpiration control and tolerance to poorly aerated saturated soil.

Compared with the Dismal Swamp flora there is a much reduced number of southern swamp species and in addition 36 per cent of these species are approaching the limits of their ranges. These facts indicate that Pocomoke Swamp is either an outlier or very near the northern fringe of the center of maximum development of the typical southern swamp.

SUMMARY AND CONCLUSIONS

The Pocomoke Swamp on the eastern shore of Maryland is of particular botanical interest because it is probably the most northern extensive area of its kind. The factors effective in maintaining the habitat and consequently the vegetation seem entirely comparable to conditions controlling the larger swamps to the south.

The swamp flora, being little disturbed by man, offers an excellent opportunity for obtaining indicators of the present edaphic, biotic, and climatic conditions of the region and at the same time a basis for comparison with the flora of other regions.

The forest is dominated by cypress, swamp black gum, and red maple

and possesses a limited growth of associated shrubs and herbs because of poor light and drainage. The greatest variation among the dominants, and associates as well, is definitely related to tide and drainage. The moisture factor results in nearly pure stands of white cedar near the upland borders and at the opposite extreme almost pure stands of cypress along the more deeply flooded river margins.

The transition from swamp to upland has the greatest variety in species of shrubs and herbs. The abundance of evergreen shrubs here indicates the xeric nature of the habitat and shows resemblances to the pocosins of the South. The open, raised, sandy areas within and bordering the swamp are characterized by numerous pine-barren species.

Parts of the upper swamp have been so devastated by fire that all plant life was destroyed. Many so-called "fire weeds" have invaded the area with other species and although retarded by fluctuating water levels these pioneer communities have initiated a hydrarch succession which should be interesting to follow in the future.

The flora of Pocomoke Swamp is more closely related to that of southern swamps than northern bogs. The preponderance of southern species bears out evidence that in the recent past, migration has been progressing from the southeastern United States. There are no indications that there will be any marked change in the swamp flora in the immediate future; it appears that it will remain essentially stable if left undisturbed.

LIST OF SPECIES COLLECTED[1]

PTERIDOPHYTA

OPHIOGLOSSACEAE

Botrychium obliquum Muhl.
Botrychium virginianum (L.) Sw.

OSMUNDACEAE

Osmunda regalis L.
Osmunda cinnamomea L.

POLYPODIACEAE

Pteridium latiusculum (Desv.) Hieron.
Dryopteris noveboracensis (L.) A. Gray
Dryopteris thelypteris (L.) A. Gray
Dryopteris intermedia (Muhl.) A. Gray
Polystichum acrostichoides (Michx.) Schott
Polypodium polypodioides (L.) Hitchc. S
Athyrium thelypteroides (Michx.) Diels.
Athyrium asplenioides (Michx.) Desv. S
Asplenium platyneuron (L.) Oakes
Onoclea sensibilis L.
Anchistea virginica (L.) Presl.
Lorinseria aerolata (L.) Presl.

EQUISETACEAE

Equisetum arvense L.

LYCOPODIACEAE

Lycopodium alopecuroides L. S
Lycopodium complanatum L. var. *flabelliforme* Fernald

SELAGINELLACEAE

Selaginella apoda (L.) Fernald

[1] Nomenclature essentially that of Gray's Manual (7th edition) except for Pteridophytes which are named as in Blomquist (1934).

Species ranging largely north of the swamp are marked N, south ranging species S, species of general distribution are unmarked.

SPERMATOPHYTA

GYMNOSPERMAE

PINACEAE

Pinus taeda L. S
Pinus serotina Michx. S
Pinus virginiana Mill. S
Pinus echinata Mill. S
Taxodium distichum (L.) Richard S
Taxodium ascendens Brongn. S
Chamaecyparis thyoides (L.) BSP. S
Juniperus virginiana L.

ANGIOSPERMAE

Monocotyledoneae

TYPHACEAE

Typha latifolia L.
Typha angustifolia L.

NAJADACEAE

Potamogeton pulcher Tuckerm.

ALISMACEAE

Sagittaria latifolia Willd.

GRAMINEAE

Erianthus saccharoides Michx. S
Paspalum laeve Michx. S
Echinochloa crusgalli (L.) Beauv.
Zizania aquatica L.
Leersia virginica Willd.
Cinna arundinacea L.
Trisetum pennsylvanicum (L.) Beauv. S
Phragmites communis Trin.
Glyceria obtusa (Muhl.) Trin.
Elymus virginicus L. var. *glabriflorus* (Vasey) Bush.

CYPERACEAE

Cyperus rivularis Kunth.
Dulichium arundinaceum (L.) Britton
Eleocharis obtusa (Willd.) Schultes.
Eleocharis tuberculosa (Michx.) R. & S. S
Fimbristylis autumnalis (L.) R. & S. S
Scirpus olneyi Gray
Scirpus lineatus Michx.
Scirpus pedicellatus Fernald. N
Eriophorum virginicum L.
Rynchospora corniculata (Lam.) Gray. S
Rynchospora macrostachya Torr.
Rynchospora axillaris (Lam.) Britton var. *microcephala* Britton S
Rynchospora glomerata (L.) Vahl. S
Carex foenea Willd. N
Carex seorsa E. C. Howe N
Carex canescens L. N
Carex stipata Muhl.
Carex crinita Lam.
Carex stricta Lam.
Carex debilis Michx. S
Carex lurida Wahlenb.
Carex lupulina Muhl.
Carex lupulina var. *pedunculata* Dewey
Carex intumescens Rudge S
Carex folliculata L. N
Carex vesicaria L. N

ARACEAE

Arisaema triphyllum (L.) Schott.
Peltandra virginica (L.) Kunth.
Orontium aquaticum L. S

XYRIDACEAE

Xyris caroliniana Walt.

COMMELINACEAE

Commelina hirtella Vahl. S

PONTEDERIACEAE

Pontederia cordata L.

JUNCACEAE

Juncus setaceus Rostk. S
Juncus effusus L.
Juncus canadensis J. Gay
Juncus acuminatus Michx.
Juncus marginatus Rostk.
Juncus aristulatus Michx. S

LILIACEAE

Oakesia sessilifolia (L.) Wats.
Lilium superbum L.
Trillium sessile L. S
Smilax tamnifolia Michx. S
Smilax walteri Pursh. S
Smilax rotundifolia L.
Smilax hispida Muhl.
Smilax lanceolata L. S
Smilax laurifolia L. S

DIOSCOREACEAE

Dioscorea glauca L. S

IRIDACEAE

Iris versicolor L.
Sisyrinchium gramineum Curtis

ORCHIDACEAE

Cypripedium acaule Ait.
Habenaria clavellata (Michx.) Spreng.
Habenaria cristata (Michx.) R. Br. S

Habenaria lacera (Michx.) R. Br.
Spiranthes gracilis (Bigel.) Beck.
Spiranthes cernua (L.) Richard.

Dicotyledoneae

PIPERACEAE

Saururus cernuus L. S

SALICACEAE

Salix nigra Marsh.
Populus heterophylla L. S

MYRICACEAE

Myrica cerifera L. S
Myrica carolinensis Mill.

BETULACEAE

Carpinus caroliniana Walt.
Betula nigra L. S
Alnus rugosa (Du Roi) Spreng.

FAGACEAE

Fagus grandifolia Ehrh.
Quercus michauxii Nutt. S
Quercus nigra L. S
Quercus phellos L. S
Quercus alba L.
Quercus rubra L. S
Quercus stellata Wang.
Quercus bicolor Willd.

URTICACEAE

Urtica procera Willd.
Boehmeria cylindrica (L.) Sw.

LORANTHACEAE

Phoradendron flavescens (Pursh.) Nutt. S

POLYGONACEAE

Polygonum pennsylvanicum L.
Polygonum setaceum Baldw. S
Polygonum hydropiperoides Michx.
Polygonum virginianum L.
Polygonum arifolium L.
Polygonum sagittatum L.

PHYTOLACCACEAE

Phytolacca decandra L.

CARYOPHYLLACEAE

Silene pennsylvanica Michx.

NYMPHAEACEAE

Nymphaea advena Ait. S
Castalia odorata (Ait.) Woodville & Wood.

RANUNCULACEAE

Thalictrum polygamum Muhl.
Anemone quinquefolia L.

MAGNOLIACEAE

Magnolia virginiana L. S
Liriodendron tulipifera L. S

LAURACEAE

Benzoin aestivale (L.) Nees

CRASSULACEAE

Penthorum sedoides L.

SAXIFRAGACEAE

Itea virginica L. S

HAMAMELIDACEAE

Hamamelis virginiana L.
Liquidambar stryaciflua L. S

PLATANACEAE

Platanus occidentalis L.

ROSACEAE

Spiraea tomentosa L.
Pyrus arbutifolia (L.) L. f.
Amelanchier oblongifolia (T. & G.) Roem.
Rosa carolina L.

LEGUMINOSAE

Cassia marilandica L.
Cassia chamaecrista L. S
Apios tuberosa Moench.
Strophostyles umbellata (Muhl.) Britton S

LINACEAE

Linum virginianum L.

POLYGALACEAE

Polygala mariana Mill. S

ANACARDIACEAE

Rhus copallina L.
Rhus toxicodendron L.

AQUIFOLIACEAE

Ilex opaca Ait. S
Ilex verticillata (L.) Gray
Ilex glabra (L.) Gray S

CELASTRACEAE

Evonymus americanus L. S

ACERACEAE

Acer rubrum L.

BALSAMINACEAE

Impatiens biflora Walt.

VITACEAE

Psedera quinquefolia (L.) Greene

Vitis labrusca L.
Vitis rotundifolia Michx. S

MALVACEAE

Hibiscus moscheutos L. S
Hibiscus oculiroseus Britton S

HYPERICACEAE

Ascyrum hypericoides L. S
Hypericum canadense L.
Hypericum gentianoides (L.) BSP.
Hypericum virginicum L.

VIOLACEAE

Viola pedata L. S
Viola cucullata Ait.
Viola lanceolata L.
Viola primulifolia L.

LYTHRACEAE

Decodon verticillatus (L.) Ell.

MELASTOMACEAE

Rhexia virginica L.
Rhexia aristosa Britton S
Rhexia mariana L. S

ONAGRACEAE

Ludvigia alternifolia L. S
Ludvigia sphaerocarpa Ell. S
Ludvigia linearis Walt. S
Ludvigia palustris (L.) Ell.
Epilobium angustifolium L. N
Oenothera biennis L.

HALORAGIDACEAE

Proserpinaca palustris L.

UMBELLIFERAE

Eryngium aquaticum L. S
Hydrocotyle umbellata L. S
Ptilimnium capillaceum (Michx.) Raf. S
Cicuta maculata L.
Sium cicutaefolium Schrank.
Oxypolis rigidior (L.) Coult. & Rose var. *ambigua* (Nutt.) Robinson S

CORNACEAE

Cornus florida L.
Cornus amomum Mill.
Nyssa sylvatica Marsh.
Nyssa biflora Walt. S

ERICACEAE

Clethra alnifolia L.
Monotropa uniflora L.
Rhododendron viscosum (L.) Torr.
Rhododendron nudiflorum (L.) Torr. S
Kalmia latifolia L.
Kalmia angustifolia L.
Leucothoë racemosa (L.) Gray S
Lyonia ligustrina (L.) DC.
Epigaea repens L.
Gaultheria procumbens L.
Vaccinium virgatum Ait. S
Vaccinium corymbosum L.
Vaccinium atrococcum (Gray) Heller

PRIMULACEAE

Lysimachia terrestris (L.) BSP.

OLEACEAE

Fraxinus pennsylvanica Marsh. var. *lanceolata* (Borkh.) Sarg.
Chionanthus virginica L. S

GENTIANACEAE

Centaurium pulchellum (Sw.) Druce S
Gentiana saponaria L. S
Bartonia virginica (L.) BSP.
Obolaria virginica L. S

ASCLEPIADACEAE

Asclepias incarnata L. var. *pulchra* (Ehrh.) Pers.

CONVOLVULACEAE

Ipomea coccinea L. S
Cuscuta compacta Juss. S

LABIATAE

Prunella vulgaris L.
Stachys tenuifolia Willd. S
Monarda punctata L.
Lycopus virginicus L.
Lycopus rubellus Moench. S

SCROPHULARIACEAE

Linaria canadensis (L.) Dumort
Chelone glabra L.
Mimulus ringens L.
Mimulus alatus Ait.
Gratiola virginiana L. S
Gerardia purpurea L. S
Pedicularis lanceolata Michx. N

BIGNONIACEAE

Tecoma radicans (L.) Juss. S
Bignonia capreolata L. S

ACANTHACEAE

Ruellia ciliosa Pursh. var. *parviflora* (Nees) Britton S

RUBIACEAE

Galium Claytoni Michx.
Diodia virginiana L. S
Diodia teres Walt. S
Mitchella repens L.
Cephalanthus occidentalis L.
Houstonia caerulea L.

CAPRIFOLIACEAE

Lonicera japonica Thunb. S
Lonicera sempervirens L.
Viburnum dentatum L.
Viburnum cassinoides L.
Viburnum nudum L. S
Viburnum prunifolium L. S
Sambucus canadensis L.

LOBELIACEAE

Lobelia cardinalis L.
Lobelia puberula Michx. S
Lobelia inflata L.

COMPOSITAE

Vernonia noveboracensis Willd. S
Elephantopus tomentosus L. S
Elephantopus nudatus Gray S
Eupatorium purpureum L.
Eupatorium serotinum Michx. S
Eupatorium hyssopifolium L. S
Eupatorium verbenaefolium Michx. S
Eupatorium rotundifolium L. S
Eupatorium pubescens Muhl.
Mikania scandens (L.) Willd.
Heterotheca subaxillaris (Lam.) Britton & Rusby S
Chrysopsis mariana (L.) Nutt. S
Solidago fistulosa Mill. S
Solidago rugosa Mill.
Solidago tenuifolia Pursh. S
Aster surculosus Michx. S
Aster vimineus Lam.
Aster lateriflorus (L.) Britton
Aster tradescanti L.
Aster paniculatus Lam.
Aster novi-belgii L.
Aster tardiflorus L. N
Erigeron canadensis L.
Baccharis halimifolia L. S
Pluchea foetida (L.) DC. S
Pluchea camphorata (L.) DC. S
Antennaria plantaginifolia (L.) Richards
Gnaphalium helleri Britton S
Eclipta alba (L.) Hassk. S
Rudbeckia laciniata L.
Bidens discoidea (T. & G.) Britton S
Bidens comosa (Gray) Wiegand
Bidens laevis (L.) BSP. S
Bidens trichosperma (Michx.) Britton S
Helenium autumnale L.
Erechtites hieracifolia (L.) Raf.
Senecio aureus L.
Senecio tomentosus Michx. S
Krigia virginica (L.) Willd.
Lactuca canadensis L.
Hieracium venosum L.

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Further Analysis of the Pea Test for Auxin

F. W. Went

(with four figures)

Introduction and methods

The pea test, although most convenient in determining the content of growth promoting substances of solutions, is little understood. So far every publication dealing with this test gave a different explanation of its mechanism (Went 1934, Jost and Reiss 1936, van Overbeek and Went 1937, Thimann and Schneider 1938).

In spite of the differences in views of the various authors, all now agree that the pea test is a differential growth phenomenon. As such it has to be studied by measuring the growth. This is not so easy, however, since it is difficult to get accurate length measurements of a strongly curved object. Van Overbeek and Went (1937) marked the pea stems with India ink before splitting; after a certain time when the major part of the growth was completed the marks, which originally were 1 mm. apart, were again measured. For the present investigation, the method was simplified by marking the stems with a suspension of lampblack in lanoline. For this purpose the stems were carefully rolled over a frame, strung with fine wires exactly 1 mm. apart and covered with a very thin layer of lanoline. Then they were split and placed in solutions of indole acetic acid. After various periods the stems (B Fig. 1) were taken out of the solution and gently pressed against a piece of paper (C), by rolling a thin glass rod (A) over them. The marks, which do not dry up, were thus transferred to the paper, and their distances apart could easily be measured. This method has many advantages. In the first place it leaves a permanent record; secondly the marks on the curved pea stem are projected in the plane of the paper, which makes measuring much easier and more accurate. After the first recording there is enough lanoline left on the stem if one or two more prints are desired. It is thus possible to measure the growth of any length of stem, without having to measure the marked intervals individually. Generally only the marks on the convex or outside (o in mm.) were transferred. By measuring the thickness of the stem (d in mm.) and the curvature (c in degrees) the length of the inside (i in mm.) was calculated: $i = o \cdot c / 114 \cdot d$. Fig. 1 shows how the marks are transferred, together with an actual record.

Experiments on the mechanism of the curvatures

A discussion of the experiments should be opened with a warning. Although the gross sensitivity of the pea may vary within certain limits

on different days, qualitatively the same curvatures are obtained. But there may be unexpected and great differences in the type of reaction. Van Overbeek and Went (1937) showed that peas, infiltrated with indole acetic

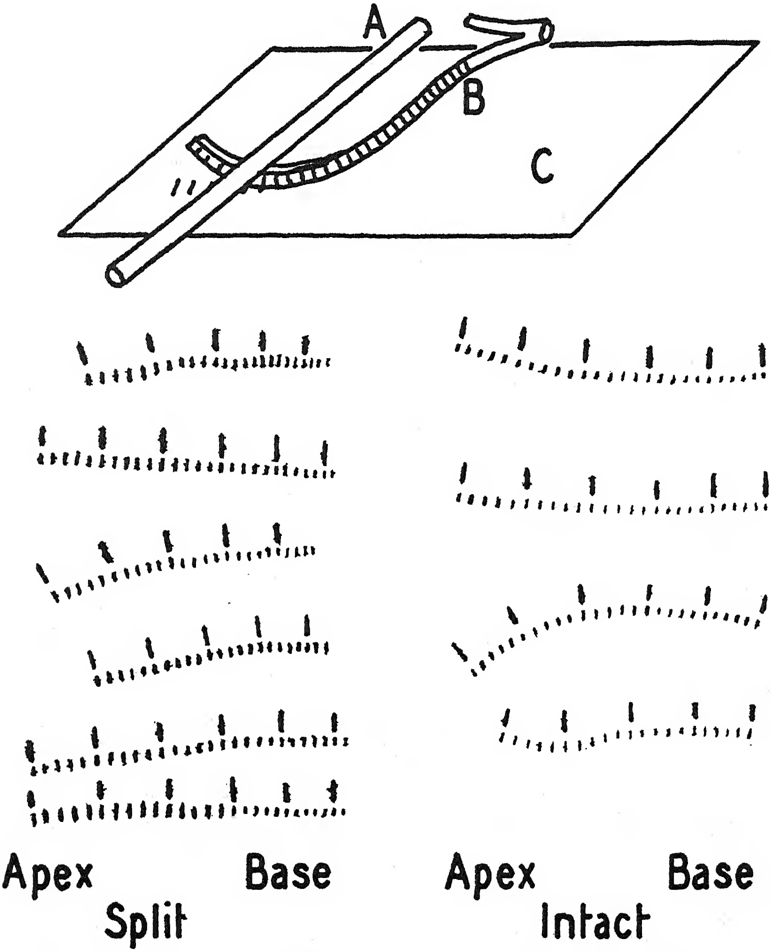

Fig. 1. *Above:* pea stem (B), which was marked with black lanoline before splitting. By gently rolling a small rod A over the stem, the marks are transferred to the paper (C). *Below:* actual record. For convenience every fifth mark is indicated by an ink mark above. The zones near the apex have grown most, in the 24 hours that they were left in indole acetic acid 4 mg./l. *On left:* marks from stems split after marking, *on right:* stems left intact.

acid immediately after splitting did not show any inward (growth) curvatures. Thimann and Schneider (1938) on the other hand claim that in two experiments the infiltrated peas showed normal inward curvatures. This experiment has been repeated innumerable times, and it was found

that in about half the cases no curvatures, in the other cases weak to good pea tests were obtained after infiltration. A general correlational analysis did not reveal the cause of these differences. Other discrepancies are the apparent activity of phenyl butyric acid on some days, and its complete inactivity on others. Also the inability of Jost and Reiss (1936) to obtain pea test curvatures, must be credited to such differences in the experimental material.

Many of the complex phenomena of the pea test have not been described yet. Still they all should be known and explainable on the basis of a valid theory. Therefore first a number of facts will be established, which will be discussed later.

Table 1 gives the summary of one experiment (several others gave the same result) in which the growth of 5 mm. zones of intact and split pea stems are compared, when placed various times after cutting and marking

TABLE 1

Etiolated pea stems cut 5 mm. below 4th node (bearing 1st leaf) and just below 3rd node, then marked and either split or left entire. Placed in indole acetic acid solutions immediately afterwards or after 4 or 9 hours washing in water. Growth in mm. of the most apical, and the next two 5 mm. zones. All figures the mean of 6–10. Plants measured 24 hours after cutting and marking.

Indole acetic acid concentration			4 mg./l.			0.5 mg./l.			0
Length of washing period between marking and placing in indole acetic acid			0	4 Hrs.	9 Hrs.	0	4 Hrs.	9 Hrs.	Control in H_2O
Entire stem		Top 5 mm. zone	4.7	4.5	3.1	4.2	3.0	2.0	1.2
		Second 5 mm. zone	3.2	2.6	1.8	3.0	1.9	0.9	1.1
		Third 5 mm. zone	1.7	1.5	0.8	1.8	1.1	0.6	0.8
		Total 15 mm. zone	9.6	8.6	5.7	9.0	6.0	3.5	3.1
Split stem	outside	Top 5 mm. zone	3.4	2.7	2.1	2.9	1.7	1.6	0.8
		Second 5 mm. zone	2.1	1.6	0.8	2.0	1.0	0.7	0.6
		Third 5 mm. zone	1.5	0.7	0.4	1.4	0.4	0.3	0.5
		Total 15 mm. zone	7.0	5.0	3.3	6.3	3.1	2.6	1.9
	Curvature		209°	240°	104°	122°	86°	25°	+88°
	Growth of inside	Total 15 mm. zone	4.6	2.3	2.1	4.9	2.1	2.3	2.4

in indole acetic acid solutions of 4 and 0.5 mg./l, and in water. Each figure is the mean of the individual measurements of 6–10 pea stems, and represents the increase in length of the zones 24 hours after marking them. A large number of conclusions can be drawn (all corroborated by other experiments).

1. When placed immediately in the solutions, the strong and the weak indole acetic acid gave approximately the same reaction as far as growth

was concerned. However, the pea test curvatures were much less in the weaker solution. But when 4 or 9 hours had elapsed before transferring the peas to auxin, the growth in the weak solution was much weaker.

2. Although the total growth was much less after 4 hours in water, the pea test curvatures in the stronger solution were considerably larger than after immediate transfer into the auxin. Together with 1 it is clear that there is no direct correlation between absolute growth of the outside and pea test curvatures.

3. The decrease in reactivity is least pronounced in the apical zones, the more basal zones have lost the power to respond to indole acetic acid after 9 hours in water. This corresponds to a very different type of curvature. When stems are placed in auxin solutions immediately after splitting, the curved zone is quite long—more than 20 mm.—and the radius of the curvature is large too. With longer intervals in water before placing them in auxin the total curvature increases or decreases, but is restricted to an increasingly shorter zone, with a decrease in the radius of curvature.

4. The reactivity to auxin of the inside is only present immediately after splitting, but after 4 hours in water and in another experiment after 2 hours already the inside fails to react at all.

TABLE 2

Alaska peas, 7 days old, cut and split in the standard manner, then infiltrated or not, and immediately or after 2 and 4 hours shaking in water transferred to an indole acetic acid solution of 4 mg./l. Curvature measured after 24 hours, means of 16–22 halves.

WHEN IN INDOLE ACETIC ACID	IMMEDIATELY	AFTER 2 HOURS	AFTER 4 HOURS
Not infiltrated	252 ± 23	391 ± 34	211 ± 23
Infiltrated with H_2O	1	88	150 ± 21
Infiltrated with indole acetic acid 0.2 mg./1	43	104	166

5. The reactivity of the outside slowly drops after cutting; the reactivity of the inside, however, drops much more rapidly, so that the pea test curvatures first increase and after that again decrease with increasing time between splitting and immersion in auxin solutions. This is also the reason why in the standard pea test the split stems are washed in water for at least 2 hours (in the present work mostly 4 hours). To show that the increased pea test curvatures after washing for some hours in water is not a single exception, table 2 presents an experiment in which the split pea stems were left in water for 0, 2 or 4 hours, before they were transferred to indole acetic acid 4 mg./l. One third of the peas was infiltrated with water, the second third was infiltrated with a solution of 0.2 mg. indole acetic

acid per liter, and the last third was left uninfiltrated. The results show that the pea test curvatures increased, when 2 hours elapsed between splitting of the peas and auxin application. After that they decreased again. In other experiments the increase in curvature was not so sudden, but continued for 4 hours at least (see table 1). In many experiments this initial rise was not found (see fig. 4). Also in the experiment of table 2, in the peas immediately placed in auxin the curved zone was long, and the radius of curvature large (6 mm.). After two hours washing the radius of curvature was much decreased (3.7 mm.), the curved zone also shortening and after 4 hours these decreases had continued (radius 3.3 mm.).

When infiltrated with either water or indole acetic acid and immediately immersed in indole acetic acid 4 mg./l., no or very small curvatures developed. That the infiltration in itself did not prevent curva-

TABLE 3

Pea test curvatures, in degrees, when peas were infiltrated either before or after splitting. The curvatures were all carried out in an indole acetic acid solution of 1 mg./l.

TYPE OF TREATMENT	CURVATURE PER STEM	NUMBER OF SPLIT STEMS
Not infiltrated, after splitting in indole acetic acid 1 mg./l.	217 ± 16	34
Infiltrated with H_2O, then split, then immediately in auxin	4 ± 3	44
Split, immediately infiltrated with indole acetic acid 1 mg./l., then in auxin	1	44
Split, after 2 hours infiltrated with indole acetic acid 1 mg./l., then in auxin	81 ± 13	34
Split, immediately infiltrated with water, then in auxin	0	44

ture is shown by those peas which were washed for 2 or 4 hours between splitting and infiltration. When placed in indole acetic acid after this period of washing good curvatures developed.

The rapid loss of reactivity is not limited to the cells along the longitudinal cut surface, but this phenomenon is also observed in the cells near the apical cut. When peas were not split, and placed in indole acetic acid 4 mg./l. immediately after cutting and marking, the two most apical 1 mm. zones elongated 0.9 and 1.0 mm. respectively. But after 4 hours washing these zones grew 0.6 and 0.9 mm. only. In the intact peas of fig. 1 this phenomenon is also very marked. The most apical 1 mm. zone has grown less than the next 5 zones. These peas were washed for $2\frac{1}{2}$ hours between cutting and placing them in the indole acetic acid 4 mg./l. solution. Thus we may conclude that the rapid loss of the ability to respond to auxin is a property of all cells close to a cut surface, whether it is a longitudinal or a cross cut. Due to the elongated form of the cells in the

pea stem we might expect the effect in the former case to be more localized than near a cross cut.

Other experiments (see e.g. table 3) indicated that it is of little importance whether the peas were infiltrated before or after splitting. Also it did not make any difference whether the infiltration took place with water or indole acetic acid, when afterwards the peas were all placed in an indole acetic acid solution. On days when the infiltrated peas gave good curvature, these were the same whether infiltrated before or after splitting. Tables 2 and 3 give additional evidence that often no auxin curvatures appear after infiltration, so that any hypothesis about the mechanism of the pea test should include this phenomenon.

If the pea test were due to a differential response of the inner and outer tissues it would be expected that the position of the split, whether near the margin or through the center, would make a great difference in the extent of the curvature. It seems hard to imagine that tearing the epidermis off one side would give any appreciable curvature at all, unless the epidermis alone were the reactive tissue. This, however, is not the case, since peeling of a halved stem which started to curve in auxin, increased the incipient curvature. Besides, the epidermis along the sides would tend to counteract the appearance of a curvature. In "pea tests" carried out with Avena coleoptiles especially it seems impossible to uphold this hypothesis since there is no inner core, and the epidermis and parenchyma cells are placed in such a way that only when the halved cylinder would roll out flat an auxin curvature would develop. And just the contrary is the case. Therefore, a crucial experiment was carried out with Avena coleoptiles. Their cylindrical form allows cutting longitudinal strips of tissue (see fig. 2), along the broad or narrow side of the coleoptile, in which the two wounded sides lie at opposite sides, symmetical in relation to the rest of the tissue, as in strips No. 1, 2, 7 and 8. The other two sides are inner and outer epidermis respectively. Such strips would be ideal for differential tissue growth curvatures, but could not give curvatures due to loss of reactivity of the cells near the wound. And indeed such strips did not show a trace of the "pea test" curvatures in indole acetic acid 2 or 4 mg./l. But whenever the wounded sides were both situated towards one side of the strip of coleoptile as in strips 3, 4, 5 and 6, fig. 2, inward curvatures resulted. In a special experiment it was determined that the narrow strips which bent outward in indole acetic acid 4 mg./l., grew a measurable amount (13% more than the water controls, measured along the outer epidermis, so that the inner epidermis must have grown still more), indicating that the outward curvature was accompanied by growth. The wide coleoptile strips

which bent inward grew somewhat more (19%) which might be expected on account of the relatively smaller effect of the wound.

In a few experiments the relation between the thickness of the split pea stem and its auxin curvature was determined. Fig. 3 combines the results of 3 experiments, and it will be seen that the curvatures of the stems from which the epidermis only has been torn off one side are almost as large as those of evenly split stems. When the growth of the zones was measured it was found that in the very wide halves the outside grew about

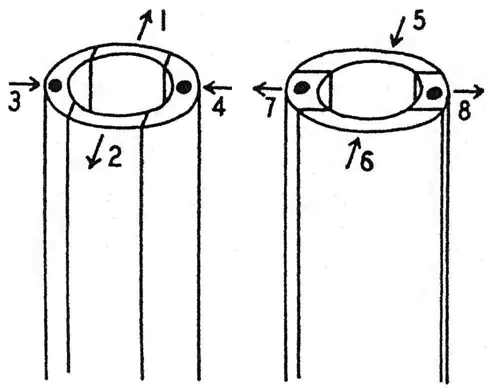

Fig. 2. Schematic picture of the way Avena coleoptiles were cut to obtain strips of tissue in which the wounded sides were symmetrically located towards the rest of the tissue (strips 1, 2, 7, and 8). The arrows indicate the sense of bending when placed in indole acetic acid 2 or 4 mg./l. The black dots represent the cross sections through the vascular bundles.

as much as an intact stem, which means that the wound was so far away from this side that it did not appreciably affect its growth. The narrower the split stem, however, the more the growth of the intact side was affected. The effect of the wound on the cut side was more nearly the same, and especially when the net effect of the indole acetic acid was calculated for thick and thin halves, the maximal differences for the inside were only 1.4 mm. against 4.3 mm. for the outside. When we consider that in the very wide and in the narrow halves the reacting inside tissues must have been cortical parenchyma, whereas in the wide and in the equal halves this was more centrally located tissue, we see that also these measurements do not support Thimann and Schneider's idea, that the central tissues would react less to auxin than the peripheral tissues. They fit in very well with the hypothesis, that the reactivity of the tissues decreases due to the wound, irrespective of where the wound is located.

Some experiments were carried out, removing the epidermis from the pea stems. Under those conditions completely different reactions were obtained. When peas were split in the ordinary way, and immediately afterwards the epidermis was removed on the side opposite the first cut surface, so that the wound effect was symmetrical on both sides of the halved stem, then distinct pea test curvatures developed; these curvatures, however,

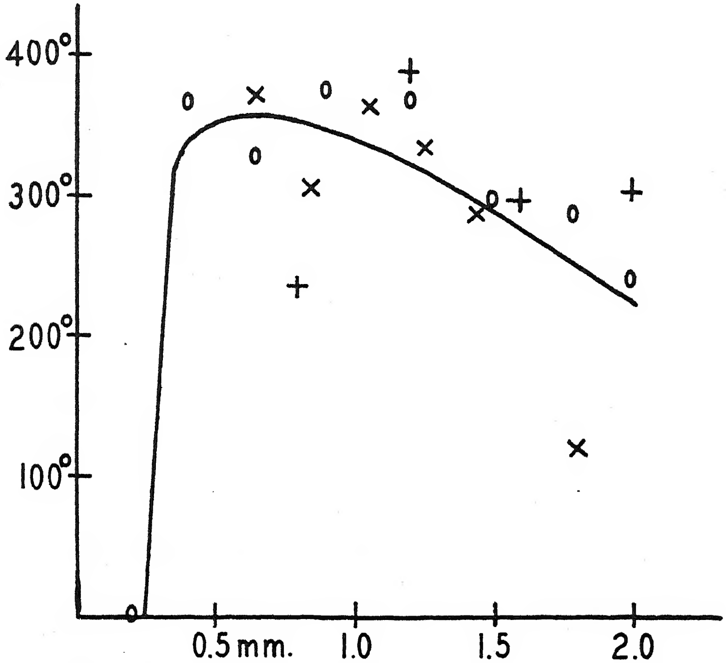

Fig. 3. Relation between thickness of the split pea stem (abscissa) and curvature (ordinate) in three different experiments, when unequally split stems have been lying in indole acetic acid 4 mg./l. for 20 hours. Each point is the mean of 10–20 observations.

appeared both in water and—somewhat larger—in indole acetic acid 4 mg./l. within 1–10 minutes after cutting. This indicates that these curvatures are primarily due to released tissue tension, and not to differential growth. If the epidermis was first peeled off, and then after 2 or 4 hours the stems were split, no pea test curvatures appeared at all (19°, 23° and 6° for 3 groups of plants of 20 halves each). Another indication that inward curvatures of the peeled halves were not due to differential sensitivity of the tissues, was found by infiltrating split stems and peeling them. Immediately the halves, which first were curved outward, bent inward, and remained so, although the halves with epidermis kept their outward curvatures, even when placed in indole acetic acid.

In the discussion the facts incorporated in the above experiments will be reconsidered. For the following experiments it is sufficient to know that there may be considerable difference in the pea test from day to day. The curvatures are due to the fact that the cells near the wound rapidly lose their sensitivity for auxin so that a few hours after cutting especially the tissues near the intact outside will respond to auxin.

EXPERIMENTS ON THE MECHANISM OF THE GROWTH REACTION

In the course of the testing of many different substances for activity in the pea test (see Koepfli, Thimann and Went 1938), it was found that in most cases a very clear distinction could be made between active and inactive substances, the latter never showing a trace of curvature. With some compounds, notably cyclohexane acetic acid and γ phenyl butyric acid, sometimes no trace of activity was found, but in other cases a few to many halved stems showed typical growth curvatures. Neither the magnitude of the curvature, nor the percentage of curved halves, however, bore any relation to the concentration used. To give an example of such an effect, the following typical experiment is quoted. The first figure in each group of 3 gives the concentration of cyclohexane acetic acid in mg./l. the second the percentage of stem halves with inward curvature, and the third curvature in degrees of halves which showed pea test curvatures. 60: 40%: 27°—30: 17%: 12°—12: 25%: 31°—6: 36%: 25°—3: 36%: 18°—1.2: 0%: 0°—0: 0%: 0°. This very clearly shows that the curvatures, although conditioned by cyclohexane acetic acid in concentrations above 2 mg./l., were limited by some other, internal factor.

It was soon found that this erratic behavior could be eliminated by washing the split stems for 4 hours in tap water before placing them in those solutions. Fig. 4, the mean of 2 experiments, illustrates the effect of washing the split pea stems for various periods. Whereas the activity of γ phenyl butyric acid completely disappears after 4–6 hours washing, the activity for low and high indole acetic acid concentrations, although falling off in the same period, still remains after 10 hours washing. In some respects this behavior resembles the effect of acid on straight growth: as long as sufficient auxin is present in the stem, any acid will activate this auxin and increase the growth, but when the auxin has disappeared, only true growth promoting substances will be able to induce further growth, and other acids are without effect (Bonner 1934, Thimann 1935).

This reasoning led to the discovery of the following phenomenon. Pea stems which had been split and washed in water for 4 hours, were for 2 hours placed either in water or in a solution of γ phenyl butyric acid of 100

mg./l. (pre-treatment). After that they were transferred to indole acetic acid solutions (after-treatment). It was found then that the pre-treatment with phenyl butyric acid had greatly increased the response to low indole acetic acid concentrations. Still, the pre-treatment by itself had not caused any visible effect. In tables 6 and 7 examples of this behavior are given.

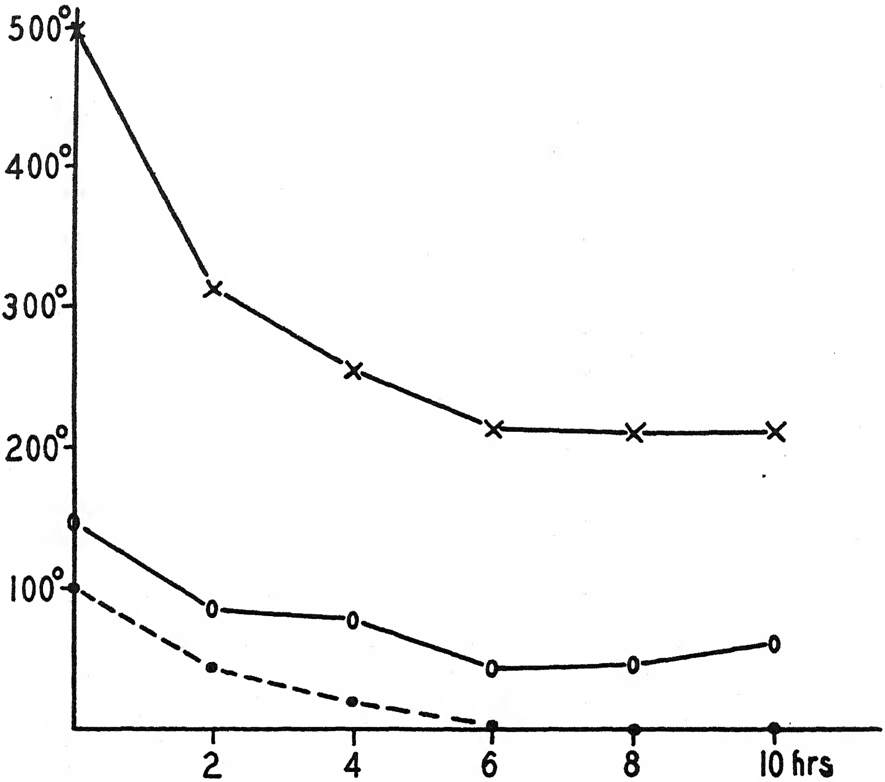

Fig. 4. Pea test curvature in degrees (ordinate), when peas are split and after various periods of washing in tap water (abscissa in hours) are placed in indole acetic acid 4 mg./l (crosses), 0.2 mg./l (circles), or γ phenyl butyric acid 100 mg./l (dots), and left in those solutions for 20 hours. Mean of two experiments. Each point represents the mean reaction of 20–40 halved stems.

It is a response which practically never fails. It also should be added that most other acids like acetic, butyric or benzoic acid do not cause a trace of such a response, so that it is not a simple acid effect.

In connection with the previous experiment the question was raised whether the effect of the phenyl butyric acid was not rather a growth inhibition, being most pronounced at the wounded side. Pea stems were marked in mm. zones and were pre-treated for 4 hours with either water or

phenyl butyric acid, and after-treated with water or indole acetic acid 0.2 mg./l. of various experiments, all giving the same results only one is reproduced in table 4. The effect of the pre-treatment is the same as if the peas had been treated with a strong indole acetic acid concentration: especially the growth of the outside is greatly increased. In another ex-

TABLE 4

Growth of etiolated pea stems, when they are split and submitted to various pre- and after-treatments.[1]

PRE-TREATMENT		AFTER-TREATMENT		GROWTH IN % OF ORIGINAL LENGTH OF	
marked, split and placed in water	in phenyl butyric acid 100 mg./l.	in water	in indole acetic acid acid 0.2 mg./l.	inside (wounded side)	outside (epidermal side)
				per cent	*per cent*
6 hrs.	—	10 hrs.	—	7.2	3.3
2 hrs.	4 hrs.	10 hrs.	—	7.9	7.3
6 hrs.	—	—	10 hrs.	6.8	7.9
2 hrs.	4 hrs.	—	10 hrs.	10.4	27.8

[1] Experiments of Dr. van Overbeek.

periment not reproduced in tabular form, it was found that pre-treatment did not have any effect on the non-split stems, whether they were placed afterwards in a strong or average indole acetic acid concentration. In the split stems there was no effect when after-treated with the high indole acetic acid concentration, neither as far as growth nor as curvature was

TABLE 5

Growth of 5 mm. long pea stem sections, in different pre- and after-treatments after cutting.[1]

PRE-TREATMENT		AFTER-TREATMENT		GROWTH IN % OF ORIGINAL LENGTH	
5 mm. pea stem sections in water	in phenyl butyric acid 100 mg./l.	in water	indole acetic acid 0.2 mg./l.	old peas	young peas
				per cent	*per cent*
6 hrs.	—	12 hrs.	—	9	22
2 hrs.	4 hrs.	12 hrs.	—	12	21
6 hrs.	—	—	12 hrs.	33	46
2 hrs.	4 hrs.	—	12 hrs.	33	50

[1] Experiments by Dr. van Overbeek.

concerned (cf. table 6). But with 0.5 mg./l. after-treatment the regular effect on the curvature was obtained. This was due to an increased response of the intact outside; the insides grew approximately the same. Statistically the difference is significant; for the upper 10 mm. it is 1.1 ± 0.33, or 3.5 times the standard deviation.

In another experiment (table 5) also kindly supplied by Doctor van Overbeek, also no effect of pre-treatment of intact stems with phenyl

butyric acid was observed, so that evidently this substance does not directly influence growth, and it can not be classified as a growth promoting substance or true auxin.

Another important observation which was made in all of the experiments, is that the growth response of the halved stems after phenyl butyric acid pre-treatment was more uniform than in the water pre-treated peas, so that the magnitude of the standard deviation was approximately 14% of the curvature for the pre-treated and 23% for the non pre-treated peas.

TABLE 6

Pea test curvatures in degrees after different pre- and after-treatments.[1]

PRE-TREATMENT WITH CYCLOHEXANE ACETIC ACID FOR 3 HOURS / AFTER-TREATMENT WITH INDOLE ACETIC ACID FOR 20 HOURS	100 mg./l.	50 mg./l.	20 mg./l.	10 mg./l.	5 mg./l.	2 mg./l.	H_2O
3 mg./l.	72	133	211	236			197
1 mg./l.	63	(62)	225	133	(83)	92	92
0.2 mg./l.	57	114	134	99	71		26
0.05 mg./l.	25	93	58	23		18	7
0.02 mg./l.	11	61	30	24			1
0.005 mg./l.	14	5	28	4			
H_2O	0	0	3	0	1		0

[1] Each figure is the mean of 14–18 half stems. The split pea stems were washed in water for 4 hours before pre-treatment.

The following experiments all serve to clearly establish this pretreatment effect and its quantitative side. It is not restricted to phenyl butyric acid, but also occurs when split pea stems are treated with true auxins, and other non-auxins like cyclohexane acetic acid. The experiment of table 6 was carried out with the latter substance. It will be seen that the curvatures obtained with low auxin concentrations as after-treatment steadily increased with increasing concentrations of cyclohexane acetic acid. In all cases, however, the solution of 100 mg./l. was lower due to some toxic effect. This toxic effect is not the same every day; sometimes 100 mg./l. will be toxic, sometimes 200 mg./l. does not show any signs of toxicity. The increased sensitivity for toxic effects seems to go parallel with a decreased response to auxin (see for seasonal variations in the pea test van Overbeek and Went 1937). The maximal curvature for each after-treatment depended also on the concentration during pretreatment: the 0.02 and 0.05 mg./l. indole acetic acid gave the largest curvatures after pre-treatment with 50 mg./l. cyclohexane acetic acid, the 0.2 and 1 mg./l. and 3 mg./l. with 10 mg./l. In summary one may

conclude that the stronger the concentration during pre-treatment the greater the effect of after-treatment with low auxin concentrations.

The effect of the pH during pre-treatment was found to be small. Thus the effect of pH on the pea test (see van Overbeek and Went 1937, D. Bonner 1938) is exerted during the after-treatment.

In further experiments based on the measurement of ca. 20,000 curved stem-halves, the quantitative relations of the "preparatory" reaction have been established. This "preparatory" reaction will be defined as that part of the chain of growth reactions, which, although without any obvious external manifestations, prepares the peas to respond, with the pea test curvatures, to very low auxin concentrations (0.1 mg./l.) which in themselves are inactive in the pea test.

The preparatory reaction requires a relatively high concentration of the active substance, even of indole acetic acid. On the other hand, the growth reaction following the preparatory reaction can be induced by exceedingly low auxin concentrations; concentrations, such as presumably exist in the normal plant. According to van Overbeek (1938) the auxin concentration in the etiolated pea stem is equivalent to 0.05 mg. indole acetic acid/l., with great variations in either direction.

We may now return to the fact mentioned before that some substances such as cyclohexane acetic acid, in most experiments cause a certain percentage of split pea stems to show growth curvatures. In those stems the auxin concentration after completion of the preparatory reaction is apparently still high enough, to act as "after-treatment." But after washing the split stems for 4 hours the auxin concentration has sufficiently dropped in most cases that no curvatures will appear any more. In one case this drop in auxin concentration was from 0.019 mg./l. indole acetic acid equivalent (see van Overbeek 1938) to 0.010 mg./l. in $5\frac{1}{2}$ hours. In experiment 80203 van Overbeek found the following decrease in auxin content: original concentration, immediately after splitting: 0.160 mg./l., after 4 hours washing 0.095 mg./l. and after 8 hours in water 0.055 mg./l. It should now be evident why the natural auxin of the pea stem is unable to induce the pea test, even though it may still cause considerable growth. The concentration of this auxin is too low to induce the preparatory reaction. Another point also may be clarified. As mentioned above auxin in very low concentrations is able to cause elongation of both inside and outside of the split stems. With such concentrations no pea test curvatures result although considerable growth may take place (van Overbeek and Went 1937). The pea test curvatures in this case are not limited by the *growth activity* of auxin, but rather the preparatory activity. Concerning the outward curvatures occurring in these low concentrations, see Discussion.

Experiments were performed to determine the effect of sugar on the component reactions of the pea test. Sucrose was used either as a pre-treatment, or was added to the auxin solutions for after-treatment. None of the sugar treatments showed any effect on the pea test curvatures obtained with low auxin concentrations. A 4% sugar solution added to the auxin caused an osmotic effect noticeable both by the decrease in rigidity

TABLE 7

PRE-TREATMENT DURING 2 HOURS WITH / AFTER-TREATMENT WITH INDOLE ACETIC ACID	H_2O	1. PHENYL ACETIC ACID				2. α PHENYL PROPIONIC ACID				3. β PHENYL PROPIONIC ACID			
		1 mg./l.	5	20	100	1 m./gl.	5	20	100	1 mg./l.	5	20	100
1 mg./l.	112	146	151	194	308	74	190	253	266	79	103	136	141
0.2 mg./l.	32	58	71	156	294	78	90	222	341	50	32	78	84
0.05 mg./l.	14	22	21	123	150	17	40	192	318	5	17	21	56
H_2O	0	0	0	16	88	0	2	32	82	0	0	0	24
CONTINUOUSLY IN PRE-TREATMENT SOLUTION	0	0	25	210	450	0	119	294	238	0	0	82	226

PRE-TREATMENT DURING 2 HOURS WITH / AFTER-TREATMENT WITH INDOLE ACETIC ACID	H_2O	4. α PHENYL BUTYRIC ACID				5. γ PHENYL BUTYRIC ACID				6. CYCLOHEXANE ACETIC ACID			
		1 mg./l.	5	20	100	1 mg./l.	5	20	100	1 mg./l.	5	20	100
1 mg./l.	112	103	76	93	124	108	122	159	232	104	163	254	199
0.02 mg./l.	32	32	35	38	33	34	47	90	102	53	67	165	156
0.05 mg./l.	14	12	5	10	8	7	26	35	142	12	29	88	116
H_2O	0	0	0	0	0	0	0	3	0	0	0	0	0
CONTINUOUSLY IN PRE-TREATMENT SOLUTION	0	0	0	0	0	0	0	0	0	0	0	0	0

of the stems in those solutions, and by the smaller curvature. In the high auxin concentrations a clear sugar effect was evident: at 2 or 3% sucrose (whether as pre- or after-treatment) the pea test curvatures were distinctly increased, suggesting that at the highest growth rates sugar became limiting, but that the preparatory reaction has nothing to do with sugar.

In this section two successive reactions, which result in the pea test curvatures have been analysed by making use of the fact that some substances may influence one and not the other of the two reactions. That both properties may be possessed by the same substance is shown in an independent way by the next experiment (table 7). Phenyl acetic, α phenyl

propionic and β phenyl propionic acids all cause good pea curvatures. If, however, the stems were taken out after 2 hours and placed in water, little or no curvatures resulted. If these pre-treated stems were placed in dilute auxin solutions the subsequent curvatures made it clear that the preparatory reaction had already taken place. In this way it was shown that the preparatory and the growth reactions differ not only in type but that with some substances they are even separated in time. This also demonstrates that the two reactions are links of a chain of reactions leading towards the pea test, and that the preparatory reaction precedes the growth reaction. The inactivity of γ phenyl butyric acid shows that a certain specificity exists for the preparatory reaction.

DISCUSSION

Now we must try to piece together the facts established in the experimental part. For the discussion it will be simplest to take the hypothesis of Thimann and Schneider (1938) as a starting point. They have disproven the hypothesis brought forward by van Overbeek and Went, that the pea test would be due to a differential auxin entry at the two sides of the split pea stem. The author is completely satisfied on this point. However, the facts presented in this paper do not agree with Thimann and Schneider's hypothesis, that the pea test is due to an innate differential reactivity of the inner and outer tissues for auxin.

To begin with all tissues in the intact pea stem seem to have the same reactivity to auxin. This is the same as Jost and Reiss (1936) have shown for Taraxacum. Perhaps the inner tissues respond slightly better than the outer tissues, but probably this is not the case. The tissue tension brought forward by Thimann and Schneider as evidence is connected with a differential elasticity of the cell walls of inner and outer tissues; the outward curvatures appear immediately and since they are completed within a few minutes they are not due to differential growth after splitting. Upon placing them in plasmolysing solution these curvatures disappear again, demonstrating that they are due to turgor, and not to growth. In the split stems the growth which still occurs in water after the initial tissue tension curvature is completed does not change the extent of this curvature, therefore, the different tissues all grow at the same rate. In fact, the curvature is so constant that de Vries (1884) could base a determination of the isotonic coefficients of solutions on the change in curvature of split stems. Whether this tissue tension is due to differential sensitivity of the tissues of the intact stem for auxin is immaterial for an explanation of the pea test, and besides it can not possibly be decided. For to determine the response of the different tissues they would have to be cut and the wounds would interfere with the normal growth rate. Besides, in the intact plant,

the inner tissues contain at least twice as much auxin as the outer layers. In one experiment the pea stems were divided into 3 strips by 2 longitudinal cuts. After extraction the inner strips, containing inner and outer tissues both gave per gram wet weight 31.°6 curvature in the Avena test, whereas the outer strips gave 15.°2 only. Another experiment gave a similar difference (28.1 against 14.8 for the outside). This is not surprising, since presumably the auxin is transported through the central cylinder, so that the inner tissues nearest the vascular elements would contain more auxin than the cortex. This fact in itself would be sufficient to account for differential growth and for the tissue tension, so that for the tissue tension curvatures of the pea stem differential response to auxin is merely an unproven hypothesis.

There is another serious objection to such a differential response of the tissues in the intact stem. When peas were infiltrated with different auxin concentrations (0.2, 1 and 4 mg./l. indole acetic acid) and allowed to grow in these solutions for 2, 4 or 8 hours, then they did not show any tissue tensions, inward or outward. This fact is also mentioned by Thimann and Schneider, but remarkably enough they consider it as an indication for differential response. But the only obvious conclusion is that the inner and outer tissues had grown at the same rate in the different auxin concentrations. Even in the 0.2 mg./l. solution, which gives only weak pea test curvatures (fig. 4, tables 6, 7), the tissue tension was released. This is a clear indication that when all cells are evenly supplied with a growth substance (the tissues were infiltrated) no differential growth takes place, and therefore, it is more likely that the tissue tension is due to differential auxin content of the inner and outer tissues.

After splitting the stem the ability of the inside to respond to indole acetic acid falls off very rapidly. After 2–4 hours its reactivity has dropped to zero. The more rapidly the auxin enters, the smaller this loss of reactivity will be; this then explains the effect of infiltration with auxin immediately before or after splitting of the peas. If the auxin acts before the drop in activity has occurred, no pea test curvatures result. An excellent confirmation of this conclusion can be found in van Overbeek and Went (1938), table 6. It will be seen that the outside of infiltrated stems has grown almost as much as in non-infiltrated stems. But the difference lies in the growth of the inside, which grows even more than the outside and much more than in any concentration in non-infiltrated stems. The criticism of Thimann and Schneider against this experiment does not hold, since in unbuffered solutions the concentration used always gave regular pea test curvatures. Besides, in the same experiment a ten times higher concentration was also used (unpublished), which caused a growth of the inside

of 7.8 mm. against 7.4 mm. in the lower concentration and 7.1 mm. of the outside. The experiment of table 2 also shows, that even when peas infiltrated with auxin immediately before or after splitting do not give pea test curvatures, they will do so when infiltrated 2 hours after the splitting, when the reactivity of the inside has decreased. In Taraxacum this loss of sensitivity of the cells bordering the wound seems to occur only when the auxin content is lowered by cutting the stems a day before the experiment (Jost and Reiss 1936).

Other peculiarities of the pea test become explainable on the basis of these facts. From the beginning, immediately after splitting the peas, there are two opposing tendencies. The first one is the loss of sensitivity of the inside tissues near the wound. This will tend to increase the curvature with increasing time between splitting and placing in auxin. But the second tendency is the loss of reactivity to auxin of the more basal zones, both of inside and outside tissues. This will restrict the curvature to a shorter zone. Now it depends which tendency is stronger whether the auxin curvature of the pea test will increase or decrease the first 4 hours after splitting, while the stems are being washed in water. Fig. 4 gives an example of an initial decrease, tables 1 and 2 of an increase in curvature within the first 4 hours.

Thimann and Schneider (1938) have laid much stress on the use of the stem-reference method for measuring the pea test curvatures, against the inflection-reference method used by the writer. In a few cases the former is indicated, e.g., when the effect of pH is under investigation (van Overbeek and Went, 1937, p. 37, D. Bonner 1938). But in most cases it complicates the interpretation of the results, since two distinct and different phenomena are being confused. One is the tendency for outward curvature, which is not restricted to the growing zone, but which is equally pronounced along the whole split section. From Thimann and Schneider's fig. 6, it even will be evident that the most pronounced outward curvature in 0.02 mg./l. indole acetic acid occurs well below the zone which will give the pea test curvature, so that the stem reference method records opposing reactions performed in different regions of the stem. Not only because this outward curvature occurs in slowly or not growing zones, it may be questioned whether it is a growth reaction at all. But also the bulk of it occurs within the first 20 minutes. So far the shortest time for the first indication of growth after auxin application has been 17 minutes (Schneider and Went 1938), but under most conditions this period is longer, and most rapid growth starts somewhat later.

Finally, this outward curvature does not or hardly occur when the split pea stems are placed in weak auxin solutions after an initial 4–6 hours

washing period in water (outward curvatures of water controls 96°, when placed immediately in phenyl acetic acid 1 mg./l. 127°, but after 4 hours washing 102°). The same phenomenon can be found in Thimann and Schneider's fig. 9, which is a most eloquent demonstration that the outward and inward curvatures are unrelated. For the inward curvatures may or may not be accompanied by an outward curvature. As a possible explanation of the outward curvatures a permeability phenomenon might be suggested, in which connection an investigation of Bouillenne (1929) might be mentioned, who worked with strips of onion leaves, which are in many respects comparable with the split pea stems. He found that certain substances in low concentrations permeated with such rapidity into the cells near the inner epidermis, that a very rapid outward curvature resulted, very much like the acid curvatures and benzofurane outward curvatures of pea stems.

In this paper the reason for the loss of reactivity of cells near the wound has not been further considered. The phenomenon itself was known, or at least postulated to explain e.g. the geotropic response of halved stems (see Went and Thimann 1937, pp. 158, 179). However, in the earlier work it was thought that the wound effect was due to auxin destruction by the wound, whereas in the present paper it was conclusively shown to be a decrease in the reactivity of the cells to auxin. It should be mentioned, that Thimann and Schneider (1938) also assume a decreased reactivity of tissue due to the influence of the wound ("damage effect") but they consider this more as a diffuse effect than one localized near the wound.

Thus in the first part of this paper it has been attempted to analyze the topographic growth relationships in the pea stem, which lead to the pea test curvatures. In the second part, the growth reaction itself has been analyzed, and has been shown to consist of two parts, which can be separated and individually measured.

There are 4 independent means of demonstrating that we have to do with 2 successive reactions, brought about by the growth promoting substances. The first one makes use of the fact, that some substances will only cause the first of the two reactions to occur, but are unable to induce the second or growth reaction proper. Such substances, which exhibit part of the properties of the auxin except the growth property, can be brought together under the name of *hemi-auxins*. It is not the purpose of this paper to discuss these hemi-auxins in detail; they only have been used as a tool. The most outstanding ones are γ phenyl butyric acid and cyclohexane acetic acid.

The second demonstration that two successive reactions, both caused by auxin, are involved in the pea test, lies in the fact that a substance like

phenyl acetic acid, before causing actual growth, will cause the preparatory reaction to occur. Thus, the two reactions can be separated in time. In indole compounds this time separation is hardly demonstrable since one seems to follow the other almost immediately.

The third difference between the two reactions is their pH sensitivity. The preparatory reaction is independent of pH, the growth reaction only occurs when sufficient undissociated acid is present inside the plant, as at low pH.

A fourth difference lies in the relative concentrations of auxin required for the two reactions. The preparatory reaction becomes negligible under 0.2 mg. indole acetic acid/l., whereas the growth reaction can be induced with less than one tenth of that concentration (table 6).

It is not possible as yet to give a satisfactory explanation of the effect of the hemi-auxins on the pea stems. It was shown that they do not affect growth by themselves. They increase the sensitivity of the cells for auxin. There are some indications that they do this by preserving or accumulating the other growth factors, of the caline or food factor type. But in another paper this will be discussed in greater detail.

As a result of this investigation the pea test can now be used for the determination of from 10 to 50 times smaller auxin concentrations than was possible before. If split pea stems are pre-treated with e.g. cyclohexane acetic acid, 50 mg./l. for 2 hours, they then will produce a curvature of 61° with 0.02 mg. indole acetic acid per liter, whereas peas not pre-treated give only 26° for 0.2 mg. auxin/l. (see table 6). The lowest indole acetic acid concentrations which can conveniently be measured with the Avena test are of the same order of magnitude (0.01 mg./l.), so that the pea test is now as suitable for the determination of low auxin concentrations as the Avena test. It has, however, one disadvantage, and that is the relatively large volume of solution required (20 cc.). The use of smaller test objects might well decrease this amount. Nevertheless for the determination of small quantities of auxin, such as occur in plant tissues, the Avena test remains indispensable. The pre-treatment has the additional advantage of making the response more uniform.

SUMMARY

The pea test curvatures, which appear when etiolated pea stems are split in their growing region and placed in auxin solutions, are due to differential growth of the tissues under the intact epidermis and the tissues bordering the wound. This is not an innate differential sensitivity of these tissues to auxin, but is due to the rapid loss of sensitivity of the tissues near the wound. If auxin reaches the cells before the loss of sensitivity

occurred, e.g., by infiltration of the split stems with an auxin solution, or by splitting them after a few hours immersion in auxin, small or no pea test curvatures result.

The effect of auxin in the pea test has been resolved into a chain of two reactions. The first is the so-called preparatory reaction, which is independent of the pH, and which can be induced by substances lacking growth activity (hemi-auxins). Indole compounds induce the preparatory reaction in relatively high concentrations (1 mg./l.). The growth reaction proper follows the preparatory reaction in time, and requires a much lower auxin concentration (appr. 0.01 mg./l. indole acetic acid).

With the aid of these new data a number of peculiarities of the pea test can be explained. A greatly improved pea test for very low auxin concentrations is described.

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A New Variety of Isoetes virginica

Norma E. Pfeiffer

(with one figure)

The species *Isoetes virginica*[1] was described in 1937 from limited material collected the previous year in Augusta County, Virginia, by Lloyd G. Carr and Edgar T. Wherry. It is a matter of interest that before other stations for the species were reported, a number of stands of an *Isoetes* now considered to be a variety of *I. virginica* were found in the Piedmont in Georgia by Joseph H. Pyron and Rogers McVaugh.

Isoetes virginica Pfeiffer var. **piedmontana,** var. nov. Folia numero 15–50, longitudine 7–15 (20) cm., gracilia, basi fuscescentia, septis crassis instructa, fibrosis periphericis numero quattuor, sex vel nonnumquam nullis instructa; sporangia oblongata, brunneo-fusca, velo angusto; macrosporae diametro 400–480 μ, variatim asperis eminulis vel brevibus cristis interdum aliquantulo ramosis ornatae; microsporae longitudine 27–33 μ, spinulosae.

Leaves 15 to 50 in number, chiefly 7 to 15 (20) cm. long, slender, brown at the base; leaf septa coarse; peripheral strands four or six in number, or entirely lacking; sporangia oblong, brown, with narrow velum; megaspores 400–480 μ in diameter, marked irregularly with low rough processes and short discontinuous ridges, sometimes branching; microspores 27–33 μ in length, spinulose.

Specimens examined:

Georgia: shallow soil about granite outcrops, Echols Mill 12 miles n.e. of Lexington, Oglethorpe Co., May 13, 1938, Pyron & McVaugh 2869 (Herb. U. Geo., Mo. Bot. Gard. Herb.). Type: same station, Feb. 15, 1938, Pyron & McVaugh 2062, and April 4, 1938, Pyron & McVaugh 2422; moist shallow soil on flat granite rock "Heggie Rock" (emersed), 8 mi. east of Appling, Columbia Co., Pyron & McVaugh 1676; shallow soil, depressions on flat granite rocks, 4 mi. s.w. of Franklin, Heard Co., April 30, 1938, Pyron & McVaugh 2835 and 2840.

Other collections which although of immature plants are probably this same variety were made in Greene Co. (P. & McV. 1645), Putnam Co. (P. & McV. 2406), Warren Co. (P. & McV. 2050), Pike Co. (P. & McV. 2293). It is apparently of fairly wide distribution in the Piedmont, with stations, of which McVaugh says "The maximum elevation is less than 1500 ft. and some of the stations are almost within the boundaries of the Coastal Plain."

The variety can be distinguished from the species chiefly on the shorter leaf length, larger leaf number, coarser septa in the leaves, and a tendency toward more open and lower markings on the megaspores. The vegetative

[1] Pfeiffer, Norma E. A new *Isoetes* from Virginia. Claytonia **3**: 29–30. 1937.

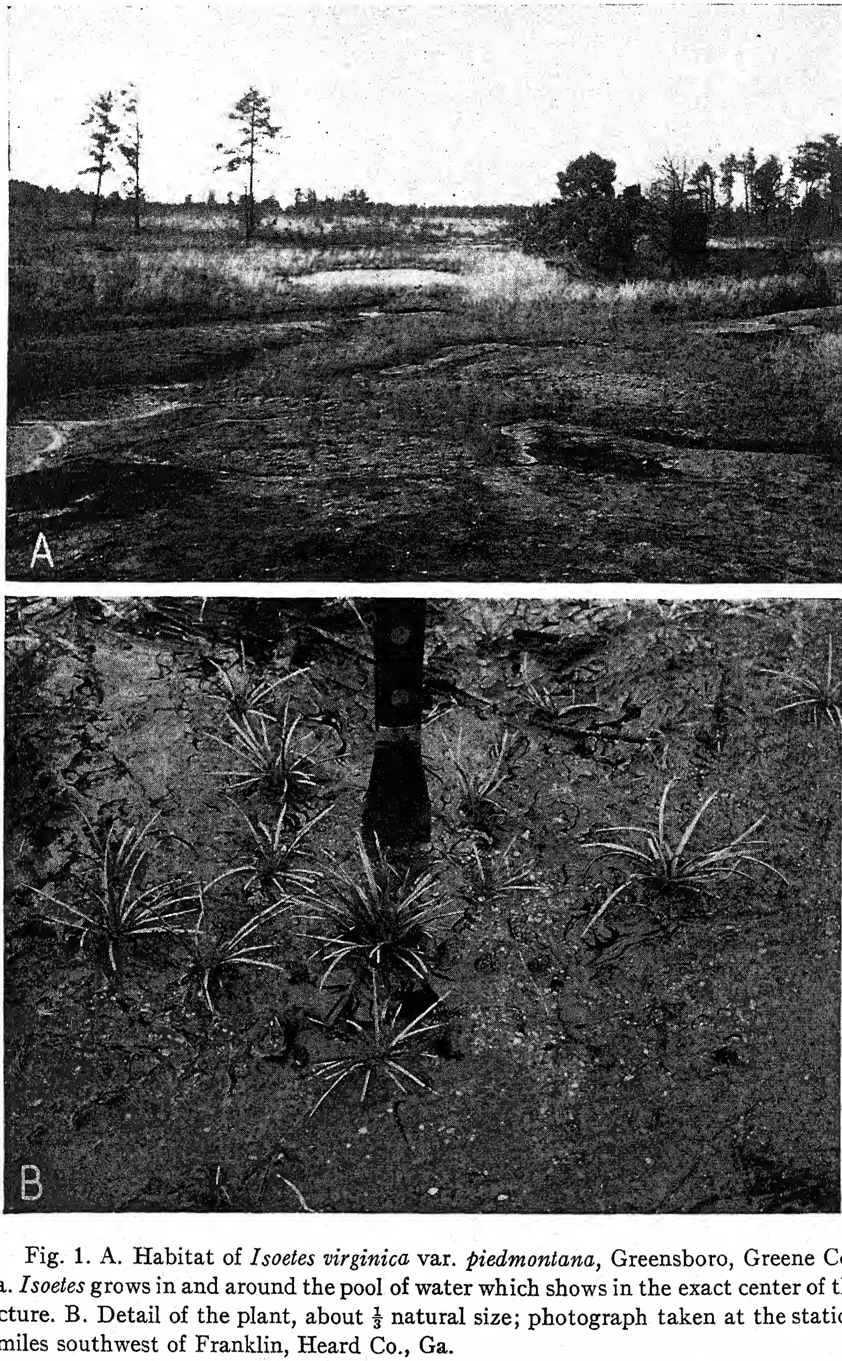

Fig. 1. A. Habitat of *Isoetes virginica* var. *piedmontana*, Greensboro, Greene Co., Ga. *Isoetes* grows in and around the pool of water which shows in the exact center of the picture. B. Detail of the plant, about $\frac{1}{3}$ natural size; photograph taken at the station 4 miles southwest of Franklin, Heard Co., Ga.

characters may be associated with the peculiar habitat, the shallow soil around the margins of flat outcrops of granite which is in distinct contrast to the "mud in a thicket bordering a meadow under water as a temporary pond in spring" in which Carr originally found the species, and the "small drainage ditch in open woodland" in Prince Edward Co., Virginia. Specimens from the latter location collected by A. B. Massey and Edith Stevens, May 13, 1938, were found on examination to resemble the previous Virginia collection and so are placed with the species.

The habitat and habit of the new variety are shown in Figure 1; the photographs were taken by Rogers McVaugh of the Division of Plant Exploration and Introduction of the Bureau of Plant Industry, who kindly obtained permission for their publication.

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Eight Undescribed Species of Melastomataceae

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Except as noted for the first species, the type specimens have been deposited in the Britton Herbarium at the New York Botanical Garden.

Tibouchina cornuta Gleason, sp. nov. Sect. *Diotanthera*: "Frutex scandens." Caules graciles, obscure 4-angulati, sparse strigosi praesertim ad angulos, pilis subulatis non glandulosis 0.4–0.7 mm. longis, ad nodos densiore setosi, pilis paulo longioribus; internodia usque 10 cm. longa superiora multo abbreviata. Petioli graciles 5–10 mm. longi, dense strigosi, pilis validis, imbricatis, 0.5–0.8 mm. longis. Laminae membranaceae, virides, subtus pallidiores, ovato-lanceolatae, usque 110 mm. longae 37 mm. latae, superiores multo minores, in quoque jugo plusminus inaequales, majoribus minores fere duplo excedentibus, acuminatae, minutissime serrulatae, ad basin cuneatae, 5-nerviae, nervis ad basin distinctis, supra strigosae, subtus ad venas substrigosae ad paginam minute pilosae. Inflorescentia pluriflora pseudo-umbelliformis, pedicellis 2–5 mm. longis. Hypanthium anguste campanulatum, 4.7 mm. longum, obscure 8–10 costatum, sparse strigosum, pilis gracilibus 0.5 mm. longis. Calycis tubus 0.5 mm. longus; sepala ligulata ultra basin late triangularem, 4.7 mm. longa, minute ciliata, parce strigosa. Petala alba, ut videtur circa 9 mm. longa. Filamenta gracilia, 5.4 vel 6.9 mm. longa; thecae anguste subulatae, leviter curvatae, 3.9 vel 5.2 mm. longae; connectiva curvata, infra thecas 0.8 vel 1.3 mm. producta ad summum filamenti, infra filamentum lobis 2 obtusis oblongis 0.8 mm. longis (in minoribus) vel 2 subulatis divergentibus recurvis 2 mm. longis (in majoribus) ornata. Ovarium summo setis circa 15 erectis subulatis coronatum; stylus leviter sigmoideus, 8.4 mm. longus.

Type, *Mexia 4296*, collected in virgin forest at Colaya, Prov. Sur Yungas, Dept. La Paz, Bolivia, alt. 1870 meters, and deposited in the Gray Herbarium. The species is intimately related to *T. capitata* Cogn. and *T. membranifolia* Cogn., also from Bolivia, and is most readily distinguished by its long sepals, those of its two relatives being triangular and scarcely 2 mm. long.

Conostegia hispida Gleason, sp. nov. Frutex 3 m. altus. Rami validi, obscure quadrangulati, dense hispidi, pilis subulatis, 2.5 mm. longis. Petioli validi, 25 mm. longi, densissime hirsuti. Laminae membranaceae, ellipticae, usque ad 22.5 cm. longae 12.5 cm. latae, abrupte acuminatae, grosse repando-dentatae, ad basin cuneatae, 5-nerviae, jugo exteriore submarginali, jugo intermedio ad basin venae mediae approximato, supra juventute sparse hirsutae mox glabrae, subtus ad paginam sparse ad venas dense setosae; nervi secundarii 8 mm. dissiti ad angulum 75° orientes. Inflorescentia terminalis, sessilis, pluriflora, dense congesta, ubique hirsuta; flores breviter pedicellati, (5 vel)

6-meri. Alabastra ellipsoidea, hirsuta, 11–12 mm. longa, rostro lineari tereti 3 mm. longo ornata. Hypanthium poculiforme, 5 mm. longum, dense hirsutum, pilis flexuosis vel crispatis, 2 mm. longis. Petala alba, triangulari-obovata, 12–13 mm. longa, 10–11 mm. lata, oblique truncata, plusminus erosa. Stamina 30 isomorpha; filamenta gracilia, 4.2–4.7 mm. longa; antherae complanatae, 2.9–3.2 mm. longae, 4-loculares, poro ventro-terminali dehiscentes, thecis infra apicem filamenti productis; connectivum elevatum exappendiculatum, supra apicem filamenti gibbosum. Ovarium inferum, 6-loculare, summo truncato-conico glabro. Stylus 7–8 mm. longus, superne leviter dilatatus; stigma capitatum.

Type, *Mexia 8430*, collected at Parroquia de Concepcion, Prov. Esmeraldas, Ecuador, alt. 105 meters. In leaf characters and pubescence *C. hispida* is similar to *C. setosa* Triana, of Colombia. It differs in leaves glabrous above and lacking bullae at the base, in its much larger flowers, in its greatly congested panicle, and in the presence of thirty stamens.

Conostegia multiflora Gleason, sp. nov. Arbor 24 m. alta. Rami 4-angulati, 4-sulcati, minute sparseque furfuracei. Petioli graciles, 15–20 mm. longi, minute stellato-furfuracei. Laminae firmulae, ellipticae vel elliptico-obovatae, usque ad 16 cm. longae 8 cm. latae, breviter abrupteque acuminatae, apice ipso obtuso, integrae vel obscure repandae, dentibus rotundatis, basi late acutae, 5-nerviae, jugo exteriore submarginali, supra virides, minutissime albo-punctatae, glabrae vel ad venas primarias minutissime furfuraceae, subtus pallidiores, ad venas minute stellato-furfuraceae ceterum glabrae; nervi primarii supra leviter impressi, subtus prominentes, secundarii utrinque plani sub angulo circa 75° adscendentes, tertiarii subtus reticulati. Inflorescentia paniculata, ramosa, multiflora, 15 cm. longa, axibus angulatis et ramis divaricatis minute stellato-furfuraceis; bracteae deciduae; pedicelli 1 mm. longi. Flores 5-meri. Hypanthium suburceolatum, 2.5 mm. longum, glabrum, in sicco ut videtur scabrellum. Calyx in alabastro ovoideus, glaber, rotundatus, 2.5 mm. longus. Petala oblonga, 4 mm. longa, 1.8 mm. lata, apice rotundata, saepe latere uno lobata. Stamina 10 isomorpha; filamenta gracilia, 2.1 mm. longa; antherae oblongae, non compressae, 4-loculares, 2 mm. longae, thecis infra insertionem filamenti in lobos 2 rotundatos breviter productis, connectivo simplici. Ovarium inferum, 7-loculare, summo subplano; stylus crassus 2.3 mm. longus, stigmate subgloboso, 0.8 mm. alto.

Type, *Mexia 8409*, collected at Parroquia de Concepcion, Prov. Esmeraldas, Ecuador, alt. 105 meters. The species is related to *C. Poeppigii* Cogn., which has acute buds, 6–8-merous flowers, and a truncate stigma.

Miconia cayumbensis Gleason, sp. nov. Sect. *Glossocentrum:* Arbor 10 m. alta. Rami teretes graciles, juventute dense sed tenuiter stellato-canescentes, demum furfuracei; internodia 3–5 cm. longa. Petioli crassiusculi, 5–8 mm. longi,

stellato-canescentes. Laminae firmulae, ellipticae vel oblongae, usque ad 16 cm. longae 6 cm. latae, breviter acuminatae, obscure remoteque denticulatae, basi acutae, 3-nerviae, jugo inconspicuo marginali neglecto, supra glabrae, subtus minutissime stellatae, pilis 0.05 mm. diam.; venae supra planae, subtus prominulae; secundariae 4–5 mm. dissitae, sub angulo fere recto divergentes; tertiariae subtus reticulatae. Inflorescentia paniculata ramosa, fere 10 cm. longa, ut rami pubescens. Flores sessiles, 5-meri. Hypanthium campanulatum, 1.7 mm. longum, obscure 10-costatum, tenuissime stellato-canescens. Calycis stellato-canescentis tubus 0.3–0.4 mm. longus; sepala late semicircularia 0.3–0.4 mm. longa, dentibus exterioribus minutis callosis. Petala anguste obovato-oblonga, 2.8 mm. longa 1.6 mm. lata, superne rotundata. Stamina dimorpha. Filamenta gracilia 3.3 vel 2.8 mm. longa. Antherae crasse lineares, thecis 2.6–2.7 vel 2.3–2.4 mm. longis, in ser. ext. poro ventro-terminali dehiscentes, in ser. int. poro terminali. Connectivum ser. ext. basi 0.6–0.7 mm. productum in lobum unum dorsalem curvatum, apicem filamenti semiamplectentem; ser. int. 0.4–0.5 mm. longum in lobum 1 dorsalem et 2 laterales divisum. Ovarium semi-inferum, 2-loculare, summo truncato-conicum glabrum. Stylus glaber, declinatus, fere 7 mm. longus; stigma capitatum.

Type, *Mexia 8285*, collected near the mouth of the Río Cayumba, Dept. Huanuco, Peru, alt. 880 meters. The width of the anther pore definitely suggests that *M. cayumbensis* belongs in the section Eumiconia. Nevertheless, when a more natural classification of this huge genus is developed, it will probably be placed near *M. longifolia* and *M. minutiflora*, now assigned to the section Glossocentrum. Most Andean species of this section have isomorphic stamens; of those with dimorphic stamens *M. longifolia* is distinguished from our species by its pli-veined leaves, and *M. minutiflora* and *M. puberula* by leaves rounded at the base.

Miconia cremadena Gleason, sp. nov. Sect. *Cremanium:* Frutex 5 m. altus; rami 4-sulcati dense subtomentosi, pilis crassis brunneis ad 1 mm. longis, internodiis usque 5 cm. longis. Petioli validi, 3–4 cm. longi, quam caules densius pubescentes. Laminae tenues, laete virides, anguste ellipticae, usque 29 cm. longae 9 cm. latae, longe acuminatae, integrae, basi acutae, 3-nerviae jugo marginali neglecto, supra glabrae, subtus ad venas primarias sicut petioli dense pubescentes, ad superficiam et venas minores villosae, pilis usque 2 mm. longis; venae secundariae sub angulo circa 80° orientes 5 mm. dissitae. Panicula ampla, ramosa, 20 cm. longa lataque, pubescens; pedicelli 1 mm. longi. Flores 5-meri. Hypanthium poculiforme, ad torum 3.2 mm. longum, carnosum primum sparse furfuraceum deinde verisimiliter glabrum, sub lente minutissime glandulosum, glandulis stipitatis 0.04 mm. longis. Calycis tubus fere erectus, 0.4 mm. longus, sinibus late acutis; sepala triangulari-ovata, a toro 1.4 mm. longa, margine scariosa; dentes exteriores late triangulares adpressi, sepala aequantes. Petala orbicularia, alba, glabra, avenia, equilatera, vix retusa, 3 mm. longa lataque. Stamina isomorpha; filamenta 3.9 mm. longa,

supra medium geniculata, glanduloso-pubescentia praesertim apicem versus; antherae obovoideae, 2.1 mm. longae, 4-loculares sed 2-porosae, septis apicem non attingentibus, thecis 1.4 mm. longis; connectivum infra thecas valde dilatatum in carinam dorsalem et ventraliter obscure 2-lobatum, saepissime pauciglandulosum. Ovarium inferum, 2-loculare, summo glabrum; stylus rectus, 6.5 mm. longus, hinc inde glandulosus, stigmate truncato 1.1 mm. diametro.

Type, *Skutch 3394*, collected in woods and thickets at Vera Blanca de Sarapiquí, Costa Rica, between Poás and Barba Volcanoes, alt. 2050 meters. In its glandular filaments it differs from all other species of *Cremanium* known to me. Its anthers are equally distinctive.

Clidemia ecuadorensis Gleason, sp. nov. Sect. *Staphidium:* Frutex glaber 3.5 m. altus. Rami obscure 4-angulati. Petioli graciles, 5–10 mm. longi. Laminae membranaceae, ellipticae, usque ad 17 cm. longae 5.5 cm. latae, apice longe caudatae, cauda lineari 25–35 mm. longa, integrae, basi acutae, 5-pli-nerviae; vena media utrinque elevata, cum venis lateralibus interioribus basi saccato-connecta; venae tertiariae insigniter reticulatae. Inflorescentiae axillares, e basi polychotomae, ramis valde divaricatis. Flores subsessiles, 5-meri, jam immaturae. Hypanthium poculiforme, ca. 2.5 mm. longum. Calycis dentes exteriores subulati, 1 mm. longi, sepala triangulari-ovata brevia multo excedentes. Petala alba decidua, immatura triangulari-ovata obtusa enervia. Antherae oblongae, connectivo non appendiculato. Ovarium inferum 3-loculare. Stylus maturus 5 mm. longus, superne conspicue dilatatus, stigmate ut videtur truncato. Fructus atropurpureus baccatus.

Type, *Mexia 8431*, collected at Parroquia de Concepcion, Prov. Esmeraldas, Ecuador, alt. 105 meters. In spite of the immature condition of the flowers, there seems little room for doubt that the species is properly assigned to *Clidemia*, within which it can not be referred to any described species. In all features of habit it is strongly suggestive of *C. japurensis* and *C. naevula*, glandular-pubescent species of Amazonia. *C. ecuadorensis* is also well characterized by the caudate appendages of the leaves.

Clidemia gracilipes Gleason, sp. nov. Sect. *Sagraea:* Frutex ramosus fere metralis. Caules superiores graciles, purpurascentes, fere glabri. Petioli graciles, divaricati, 1–4.5 cm. longi, inferne fere glabri, superne pubescentes, pilis incurvis 0.1 mm. longis. Laminae membranaceae atrovirides, in quoque jugo saepe inaequales, ovatae, majores 12 cm. longae 6 cm. latae, minores 4 cm. longae, 2 cm. latae, superiores vix reductae, acuminatae, vix serrulatae et minute ciliatae, basi late rotundatae vel cordulatae, 5-nerviae, supra fere glabrae, albo-punctatae, subtus ad primarias sicut petioli pubescentes, ad superficiem glabrae. Paniculae laxae, ramosae, ad 10 cm. longae, axibus minute sparseque hirtellis, ramis gracillimis elongatis divaricatis glabris; pedicelli ut videtur elongati, pedicellis veris 1 mm. longis bracteis 2 subulatis vix 1 mm.

longis sustentis. Flores 4-meri. Hypanthium campanulatum, purpureum, ad torum 2.6 mm. longum, minutissime pubescens, pilis incurvis 0.04 mm. longis. Calycis tubus patulus, 0.3 mm. longus; sepala late triangularia e sinibus rotundatis, 0.7 mm. longa, acuta; dentes exteriores crasse subulati, divaricati, 1 mm. longi. Petala alba, oblongo-ovata, 2.6 mm. longa, obtusa, latere tecto obscure crenato. Stamina 8 isomorpha; filamenta crassa, glabra, 1.4 mm. longa antherae oblongae, obtusae, 2-loculares, 1.6 mm. longae, connectivo simplici. Ovarium inferum, 3-loculare, summo plano glabro. Stylus gracilis, glaber, 4.8 mm. longus, stigmate truncato.

Type, *Mexia 9262*, collected in partial shade at Santa Maria, District Choapam, Oaxaca, altitude 1500 m. *Clidemia gracilipes* is closely related to *C. cymifera* Donn. Sm. of Guatemala, agreeing with it in general habit, style, stamens, and calyx. *C. cymifera* differs from ours in having much larger petals, a four-celled ovary which is only two-thirds inferior, much shorter panicles, thicker leaves, and stellate pubescence.

Blakea Mexiae Gleason, sp. nov. Sect. *Eublakea:* Arbor 12 m. alta. Rami teretes, juveniles arcte ferrugineo-tomentosi, pilis barbatis 0.5–1 mm. longis, pilis simplicibus 1–2 mm. longis intermixtis, vetustiores glabrescentes. Petioli 10–15 mm. longi ferrugineo-tomentosi. Laminae subcoriaceae pallide virides ellipticae, usque ad 12 cm. longae 6 cm. latae, acuminatae, integrae, basi cuneatae vel acutae, 3-nerviae, jugo marginali praetermisso, supra juventute ferrugineo-tomentosae mox glabrescentes vel ad venas prope basin persistenter pilosae, subtus ad venas primarias ferrugineae. Flores axillares solitarii, pedicello 2–2.5 cm. longo. Bracteae exteriores rotundae, 22 mm. longae 18 mm. latae, breviter apiculatae, multinerviae, tenuiter ferrugineae, interiores oblongo-spathulatae, 18 mm. longae, acutae. Hypathium suburceolatum, 6 mm. longum, ferrugineo-tomentosum. Calycis lobi late triangulares, 5 mm. longi, mucronati. Petala staminaque non visa.

Type, *Mexia 8320*, collected along the Río Huallaga above Cayumba, Dept. Huanuco, Peru, alt. 830 meters. *Blakea Mexiae* is related to *B. Spruceana* Cogn. and *B. paludosa* Gl. and is distinguished from both by the barbellate pubescence.

The New York Botanical Garden

INDEX TO AMERICAN BOTANICAL LITERATURE

The aim of this Index is to include all current botanical literature written by Americans, published in America, or based upon American material; the word America being used in the broadest sense.

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The Structure and Development of the Apical Meristem in the Shoots of Taxodium distichum[1]

G. L. CROSS

(WITH 25 FIGURES AND PLATES 8 AND 9)

Renewed interest in meristem has been stimulated by the researches of Schüepp (1926), Helm (1932), Louis (1935), Foster (1935, 1938), Kaplan (1937), and many others. Much of the recent work has been done with angiosperms, but the papers of Korody (1937), Härtel (1938), and Foster (1938) have shown the need for comparative work in the more primitive groups. The present paper deals with apical meristem in the shoots of *Taxodium distichum* Rich. Interest in this species was stimulated by the dearth of literature concerning the morphology of its highly complex shoot system, and by the confused and conflicting reports regarding the structure of its shoot apex (Korschelt, 1884; Groom, 1885). Although emphasis here is placed on the structure of the apical meristem in expanding deciduous and permanent shoots, the origin of the shoot apex[2] of certain of the deciduous shoots is described briefly.

MATERIALS AND METHODS

Materials were collected from two trees growing on the campus of the university of Oklahoma, Norman, and from trees growing in the flood plain forests of southeastern Oklahoma (McCurtain County).[3] Collections on the campus were made every third day throughout the season of 1937 extending from March 1 to September 1. The materials were killed and fixed under reduced pressure in a solution of 5 per cent commercial formalin and 6 per cent glacial acetic acid made up in 70 per cent

[1] Contribution from the Botanical Laboratory, University of Oklahoma, No. 55.

[2] In an effort to secure uniformity in terminology, "shoot apex" will be used to designate the apical region of the axis (Foster, 1938, footnote 2).

[3] Collecting trips were financed in part by a University Research Grant.

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ethyl alcohol. A series of tertiary butyl alcohols were used for dehydration and clearing, and the usual technique of embedding in paraffin (56° C.) was employed. Serial sections, longitudinal and transverse, were cut 8–10μ in thickness. Safranin and Fast Green F. C. F. were used in staining (Cross, 1937a).

The drawings were prepared with the aid of a camera lucida. A 4.3 mm. fluorite oil immersion objective and an 8× periplan ocular were used in making the photomicrographs, with the exception of Plate 8, figure 10, for which a 16 mm. apochromatic objective was used.

GENERAL FEATURES OF THE TWIGS

It is generally known that *Taxodium distichum* produces deciduous shoots which absciss and fall from the permanent twigs at the end of each season of growth (Henry, 1837; Coulter, 1889; Velenovský, 1905; Bernard, 1926; Doak, 1935), although apparently no description of the initiation and development of the deciduous shoots has appeared in the literature.

The general features of the twigs have been described in an earlier paper (Cross, 1939), in which four types of deciduous twigs, classified with respect to place of origin and time of expansion were listed, viz., those which arise exogenously in the axils of the upper scale-leaves of the expanding permanent twig, and expand with the parent twig; those which are formed "pseudo-endogenously" in the lower scale-leaves of the permanent twig, and expand one year later; those which arise endogenously near the base of the lower scale-leaves and scales of the permanent twig; and those which arise in the axils of the lower scales of pre-existing deciduous shoots.

A consideration of Plate 8, figures 1–6, should be of aid in understanding the shoots of *Taxodium.* Figure 1 shows an apparent terminal, but actually lateral, bud of a permanent twig. To the left in the illustration is a young megasporangiate strobilus. Another bud of a per-

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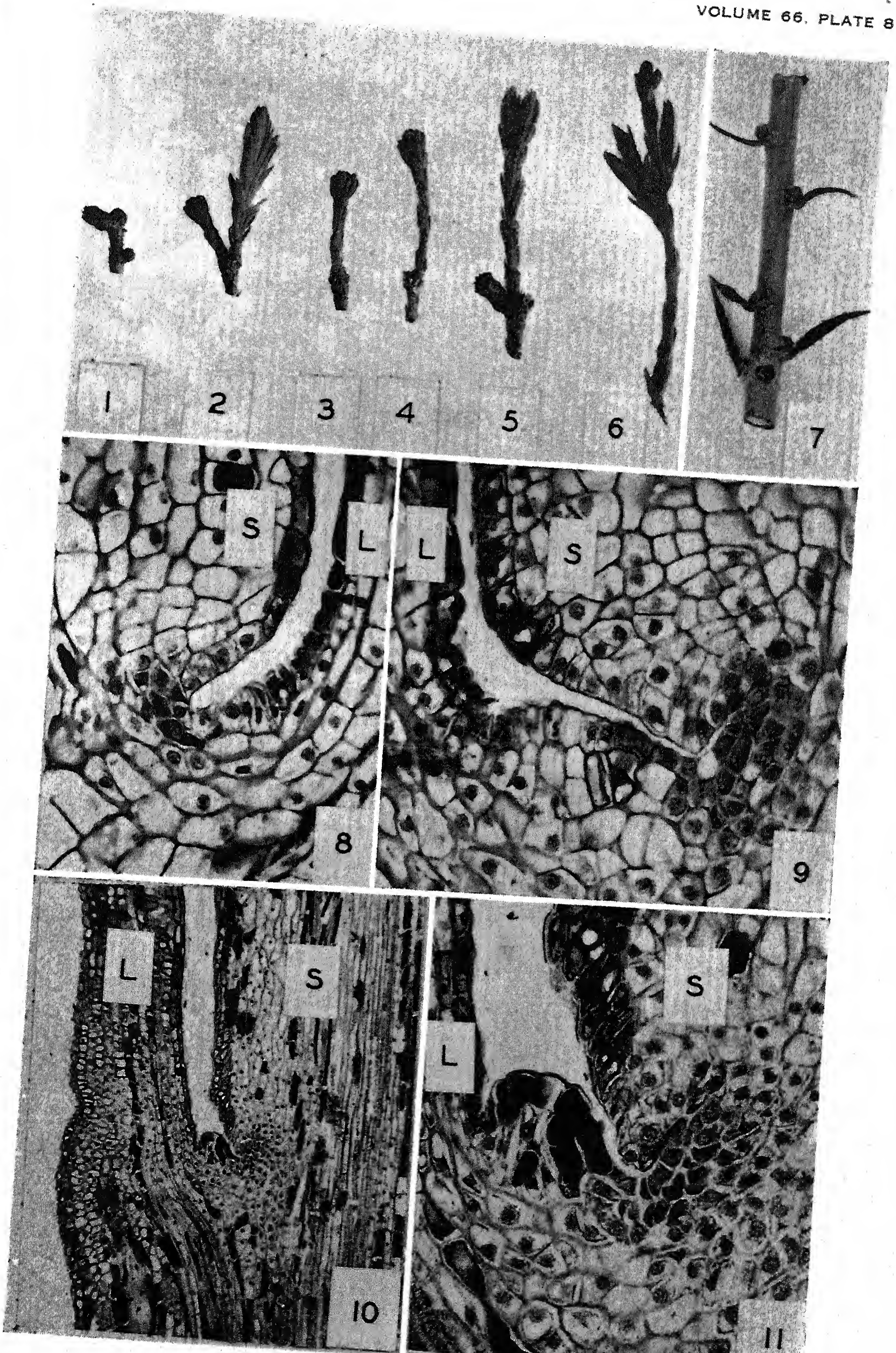
Explanation of Plate 8

All photographic work was done by William Felkner, Norman, Okla.

Figs. 1–6. A series illustrating the expansion of a permanent twig; explanation in text. ×1¼.

Fig. 7. Dormant buds of "pseudo-endogenous" axillary deciduous shoots showing splitting of the overlying cortical tissue. ×2.

Figs. 8–11. Longisections of primordia of buds of "pseudo-endogenous" deciduous shoots in various stages of development; *l,* leaf of parent shoot; *s,* stem of parent shoot. Figs. 8, 9, 11, ×220. Fig. 10, ×55.



CROSS: TAXODIUM

manent twig appears a short distance removed from the apex on the right side of the parent twig. Figure 2 illustrates the expansion of a bud of a permanent twig (to the left) and of a deciduous twig (to the right). Figures 3–6 show permanent twigs in various stages of expansion. Figures 5 and 6 show the expansion of exogenous axillary deciduous shoots from the distal portions of the permanent twigs. A twig the size of the one shown in figure 6 will have, in the axils of many of its proximal scale-leaves, the primordia of "pseudo-endogenous" deciduous shoots

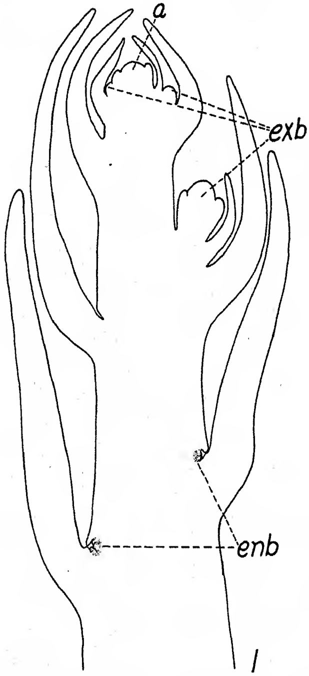


Fig. 1. Diagram illustrating longisection of expanding permanent shoot with buds of axillary deciduous twigs; *a*, apical meristem; *exb*, primordia of buds of exogenous deciduous shoots; *enb*, primordia of buds of "pseudo-endogenous" deciduous shoots.

(Cross, 1939), but these, in contrast to the exogenous shoots, do not expand at the same time that the permanent twig expands. Their expansion is delayed until the following spring and, in some cases, longer.

THE INITIATION OF THE "PSEUDO-ENDOGENOUS" BUDS

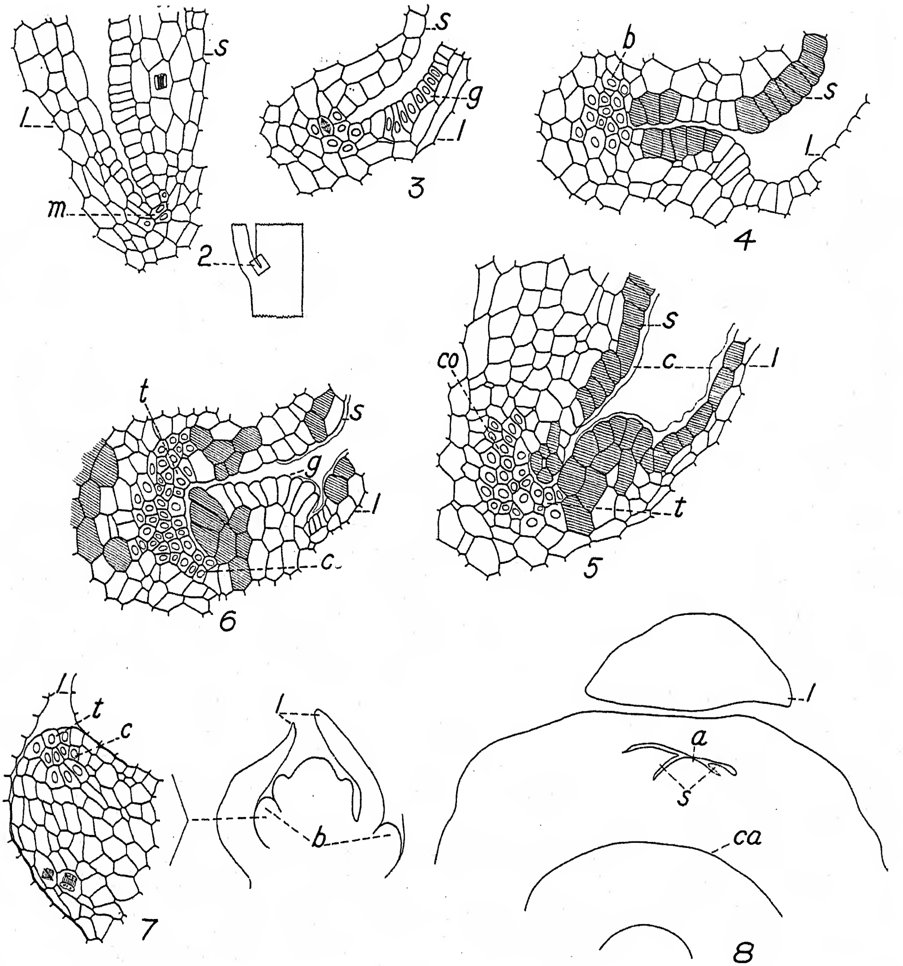
A diagram of a longitudinal section of a permanent twig showing the location of primordia of the two types of axillary deciduous shoots is shown in figure 1. In the axils of three of the more distally placed leaves are the primordia of exogenous deciduous shoots. The deciduous shoots

are formed early in the spring—in some cases before the expansion of the parent bud. They expand at the same time that the parent bud expands, and they absciss in the fall following their expansion. Thus initiation, expansion, and abscission usually occur during the same growing season. The exogenous deciduous shoots (fig. 7) present no unusual features of initiation or developement.

In the axils of two of the proximal leaves in figure 1 may be seen the primordia of deciduous shoots, which for convenience in making distinctions, have been termed "pseudo-endogenous." The initiation of these buds is delayed, in most cases apparently until the first two weeks in June, although the time of their formation varies somewhat with their distance from the apex of the permanent shoot. They develop during the summer, are dormant during the autumn and ensuing winter (Plate 8, fig. 7), and finally expand the next spring—one year after the parent twig has expanded and nearly one year after the neighboring exogenous buds have expanded. In contrast to the exogenous buds, the "pseudo-endogenous" buds are initiated the first year, but expand and absciss the second year.

"Pseudo-endogenous" buds are formed in the axils of many, but not all, of the proximal leaves. One of the first indications of their initiation is the periclinal division and enlargement of the cells of the cortex immediately above the axil of the leaf (fig. 2). As a result of these cellular divisions the cortex enlarges and crowds the leaf outward, leaving a narrow axillary slit in the bottom of which the apical meristem of the bud will be initiated (figs. 3–6; Plate 8, figs. 8–11). The division and enlargement of the cells of the cortex is usually accompanied or succeeded by a distinctive behavior of an area of the cells on the adaxial surface of the subtending leaf (fig. 3; Plate 8, fig. 8). These cells usually elongate considerably in a plane perpendicular to the surface of the leaf and form a glandular appearing mass, the surface of which is frequently elevated by periclinal and oblique divisions of the constituent cells. The elevated portion becomes closely appressed to the epidermis of the permanent shoot (figs. 4–6).

The cells of the epidermis and cortex below the bottom of the axillary slit remain meristematic (figs. 2, 3) during the developmental stages just described. Their protoplasts stain densely and dividing cells are easily demonstrated (fig. 3; Plate 8, fig. 8). At this stage, nearly median sections show that the epidermal cells in the bottom of the slit undergo repeated anticlinal divisions. The derivatives of these divisions become the tunica of the young bud (figs. 5, 6). It is shown later that the tunica



Figs. 2–6. Median longisections through axils of leaves, showing origin of apical meristem of "pseudo-endogenous" deciduous shoot; *l*, leaf; *s*, stem; *m*, meristematic cells; *g*, glandular cells; *b*, primordium of bud; *t*, tunica; *co*, corpus; *c*, cuticle. ×165.

Fig. 7. Nearly median longisection of apical meristem of young exogenous deciduous shoot. ×165.

Fig. 8. Transection above node of permanent shoot showing embedded "pseudo-endogenous" bud of deciduous twig; *ca*, cambium. ×41.

usually maintains its identity until the bud becomes dormant. During the initiation of the tunica certain epidermal cells on the axis, above the young bud, and on the adaxial surface of the subtending leaf, become filled with a densely staining material. Such cells are indicated by hatching (figs. 4–6).

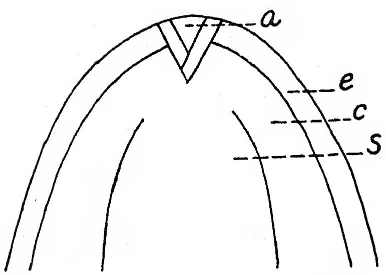
The cells of the tunica then enlarge periclinally, thus increasing the surface area of the apical meristem and widening the bottom of the axillary slit. However, concomitant enlargement of the cells in the stem and in the subtending leaf keep the slit from opening, and the epidermal cells belonging to the portion of the stem immediately above the young axillary bud are soon seen to extend as a lobe down over the bud (figs. 5, 6). During these developmental phenomena, increased mitotic activity in the cells immediately below the tunica results in the initiation of a corpus (figs. 5, 6). The rapidly enlarging lobe of the parent stem above the bud and the continued growth of the glandular mass on the adaxial surface of the subtending leaf sometimes results in an overlapping of these structures (fig. 5). More frequently the upgrowth from the leaf is more vigorous and dominates the lobe from the stem so that the latter is flattened and pressed upward (fig. 6).

When the surface area of the young bud has reached an extent approximately equal to that indicated in figure 6, the first foliar appendages are formed. These consist of two fleshy scales which arise almost simultaneously, nearly opposite each other, in a plane approximately perpendicular to the axis of the permanent twig. Transections prepared at this stage are often confusing for they give the false impression that the bud is endogenous (fig. 8). Details concerning the origin of the scales or of the immediately succeeding foliar structures were not obtained. However, it may be well to remind the reader that abscission of the deciduous shoot will ultimately occur in a plane above the first scales (Doak, 1935; Cross, 1939) and that buds of deciduous shoots will finally be formed in the axils of one or more of the scales.

The development and emergence of the bud from its sunken position in the axillary slit was observed. As the bud increases in size there is much cracking and uplifting of the overlying portions of the stem and leaf (Plate 8, fig. 7).

GROWTH AT THE APEX OF THE SHOOTS

Apparently the earliest recorded work on the structure of the apical meristem of *Taxodium* is that of Korschelt (1884), who described and prepared illustrations of surface and longitudinal views of the shoot apex of *T. distichum*. Korschelt interpreted apical growth as occurring through the activity of a single tetrahedral apical cell, similar in many respects to apical cells found in cryptogams. Groom (1885), working with the apices of "strongly growing lateral shoots" of *T. distichum*, described: (1) a sharply delimited dermatogen in which he never observed periclinal



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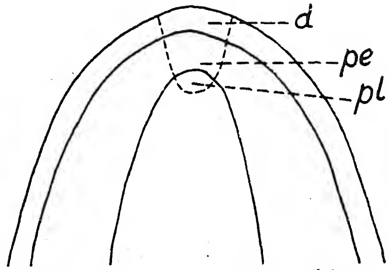

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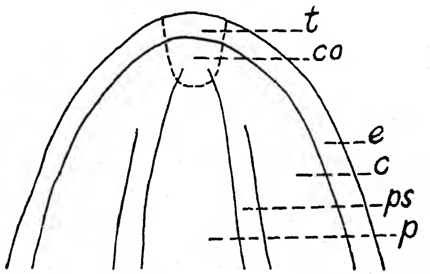

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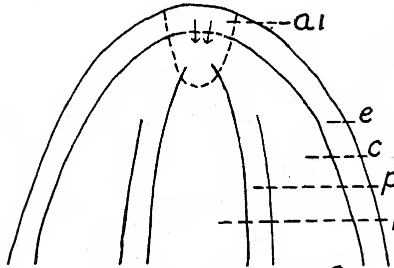

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Fig. 9. Diagram of longisection of shoot apex prepared from Korschelt's (1884) description; *a*, apical cell; *e*, epidermis; *c*, cortex; *s*, stem.

Fig. 10. Diagram of longisection of shoot apex prepared from Groom's (1885) description; *d*, dermatogen; *pe*, periblem; *pl*, plerome.

Fig. 11. Diagram illustrating structure of shoot apex of permanent and some deciduous shoots as seen in longisection; *t*, tunica; *co*, corpus; *e*, epidermis; *c*, cortex; *ps*, provascular strand; *p*, pith.

Fig. 12. Diagram illustrating structure of shoot apex of certain deciduous shoots as seen in longisection; *ai*, periclinally dividing apical initials indicating lack of distinction between tunica and corpus.

divisions; (2) a somewhat irregular periblem; and (3) a plerome dominated by 1–3 initial cells. Groom did not specify whether he worked with permanent or with deciduous twigs. In general his results are in agreement with the earlier work of Strasburger (1872) who made a comprehensive study of the stem apices in several groups of gymnosperms. However, Strasburger recognized that irregularities in the behavior of the dermatogen, periblem, and plerome are likely to occur. According to Karsten (1886) the stem apex of the seedling of *T. distichum* possesess a distinct plerome terminated by a single initial, a periblem, and a dermatogen which exists as a continuous layer but is not genetically independent of the periblem. The interesting differences of opinion developed by Korschelt (1884) and Groom (1885) concerning the structure of the shoot apex of *Taxodium* obviously are worthy of reinvestigation.

Perhaps at the outset, the fact should be emphasized that the structure of the shoot apex as described in this paper is not in accord with the earlier reports (Korschelt, 1884; Groom, 1885). The differences can best be understood by reference to figures 9–12. Figure 9 is a diagram which illustrates the type of apical growth as interpreted by Korschelt (1884) for *Taxodium*. The entire shoot is here referred in origin to the activity of a tetrahedral apical cell. The opposing view, developed by Groom (1885), is represented in figure 10, where the shoot is depicted as arising through the activity of three discrete histogens—the dermatogen, periblem, and plerome. The interpretations suggested in the present paper are summarized in figures 11 and 12. Figure 11 illustrates a condition which seems to be fairly constant for permanent shoots, although it was found in less than one-half of the deciduous shoots. In contrast to Groom's account, the periblem and plerome are not distinguishable as separate histogens at the shoot apex and the entire apical meristem is equivalent to an angiospermous shoot apex of the type possessing a one-layered tunica and a central corpus. Figure 12 represents a condition which seems to occur frequently in deciduous shoots but infrequently, or perhaps never, in the permanent twigs. In this type of apex the identity of the tunica is lost or is not maintained constantly. Periclinal divisions occur in the outer layer at or near the apex and the internal derivatives augment the underlying meristematic mass. This condition approaches that described for many gymnosperms (Strasburger, 1872; Koch, 1891; Korody, 1937; Foster, 1938). The significance of this variable apical growth (figs. 11, 12) is discussed later.

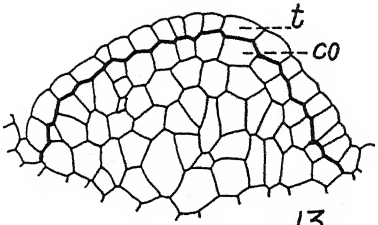
The shoot apex of *T. distichum* is circular in transection. The average diameter of fifty apices, taken at a plane equidistant from the apex and the top of the youngest foliar primordium, is 140μ in deciduous shoots and 170μ in permanent shoots. Measurements of various deciduous shoots did not reveal any constant difference in size. The longitudinal configurations of the apices of deciduous and permanent twigs are illustrated in figures 13–22. The average height of the shoot apex measuring from the tip of the axis to the upper surface of the youngest foliar primordium was about 100μ in the deciduous shoots and 80μ in the permanent shoots.

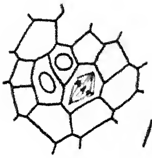
THE SURFACE LAYER OF THE APICAL MERISTEM

As stated earlier, the stem apices of the axillary deciduous shoots are characterized by an early differentiation of a peripheral tunica and central corpus (figs. 6, 7). That this is true of the exogenous deciduous

shoots as well as of the endogenous ones has been confirmed by a careful study of numerous buds in the primordial stage. Observations of a limited number of very young buds of permanent shoots indicate that they possess an organization similar in most details to that found in the primordia of exogenous deciduous shoots (fig. 7). Thus a similar basic architecture (tunica and corpus) is found in the shoot apices of all primordial buds on the permanent twigs of *Taxodium.* An investigation of the axillary buds which develop on deciduous shoots has not been made. The identity of the tunica and corpus apparently is maintained in all resting buds. The condition of the apical meristem of a dormant bud of a "pseudo-endogenous" deciduous shoot is shown in figure 13. Here the one-layered tunica (delimited by a heavy line in the illustration) appears as a distinct layer over the somewhat massive corpus. Examination of a large number of resting buds has failed to reveal evidence of any but anticlinal divisions in the tunica. However, during shoot expansion, considerable variation in structure of the shoot apex can be demonstrated. Over fifty deciduous shoots were sectioned for study and of these, approximately one-half were found to have well organized tunicas agreeing closely in most features with those depicted in figures 14 and 16. No indication of an apical cell, as described by Korschelt (1884) was found in any of the sections. Occasionally groups of conspicuously large cells were found at the apex (Plate 9, fig. 1). Studies of transections revealed that these rather large apical initials occur in groups of three or four; they are similar in size, and are characterized by somewhat greater mitotic activity (fig. 15). It seems apparent that apices of the type shown in figures 14 and 16 are essentially equivalent to those present in certain angiosperms such as *Scrophularia nodosa* L., where a one-layered tunica has been reported (Schmidt, 1924).

In slightly less than 50 per cent of the deciduous shoots examined, periclinal divisions in the cells of the surface layer of each shoot apex had interrupted the continuity of the tunica (figs. 17, 18; Plate 9, fig. 2). The divisions seem to vary considerably with respect to the location and extent of their occurrence. In figure 17 a cell of the surface layer to the left of the apex has divided periclinally and the outer derivative has divided anticlinally. Elsewhere at the apex an easily delimited dermatogen is present. Although decisive evidence could not be obtained it seems reasonable to assume that in many cases the continuity of the dermatogen is only occasionally interrupted by such periclinal divisions and that this outer layer is again organized after each periclinal division. Thus





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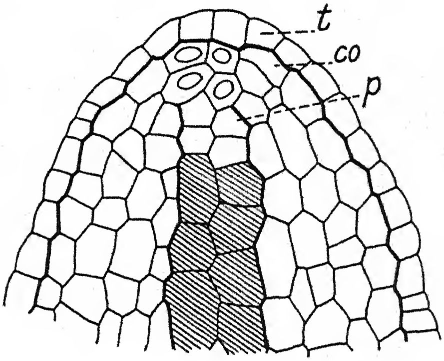

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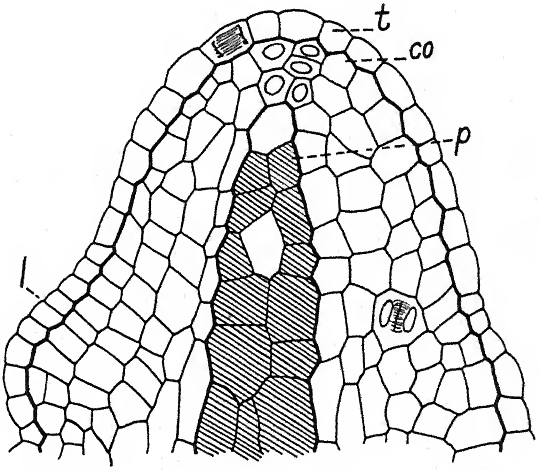

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Fig. 13. Nearly median longisection of shoot apex of dormant bud of deciduous shoot; *t*, tunica; *co*, corpus. ×330.

Fig. 14. Median longisection of shoot apex of expanding "pseudo-endogenous" deciduous shoot; *p*, pith initial. ×330.

Fig. 15. Surface view of apex of deciduous shoot. ×330.

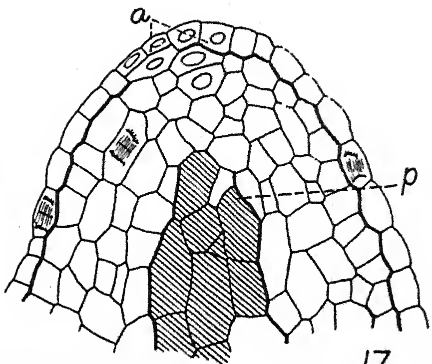
Fig. 16. Median longisection of shoot apex of expanding exogenous deciduous shoot; *l*, primordium of leaf. ×330.

an apex with apparently discrete histogens might have occasional periclinally dividing cells in the surface layer. A statistical study based upon the observation of a large number of deciduous shoots should yield valuable data. Figure 18 indicates that in certain deciduous shoots periclinal divisions may occur extensively in the surface layer of the shoot apex. The cell-complex at the tip of this shoot has clearly arisen either from two successive periclinal divisions of a pair of surface cells, or from the periclinal and anticlinal divisions of a single cell. The internal derivatives of these divisions augment the corpus. A similar condition is shown in Plate 2, figure 2. This condition is suggestive of the apical initial group described by Foster (1938) for *Ginkgo biloba*. However, in contrast to *Ginkgo*, and many other conifers (Koch, 1891; Korody, 1937), periclinal divisions in the surface layer of the stem apex of *Taxodium* are confined to the apical portion of the meristem. Only anticlinal divisions occur in the lateral portions of the surface layer; in this respect the shoot apex of *Taxodium* may be regarded as more highly organized than that of the other genera; it is transitional between the condition which obtains in *Pinus* and in certain angiosperms.

Longitudinal sections of twelve permanent shoots were compared with the sections of the deciduous shoots. The evidence appears conclusive that the prevailing condition in the shoot apex of the permanent twigs is characterized by a well organized tunica (fig. 22; Plate 9, fig. 3). Evidence of periclinal divisions could be found in only one shoot (fig. 21) and here the interpretation is open to doubt. However, in the light of the information obtained from the deciduous shoots, it would not be surprising if periclinal divisions were found to occur infrequently in the apical surface layers of permanent shoots. It should be mentioned that the interpretation of the apex shown in figure 22 agrees in part with the description by Groom (1885), except that Groom reported a distinct periblem and plerome. It is probable that Groom worked with expanding permanent shoots.

The apices of several proliferating shoots, which seemed to be intermediate with respect to external form (Cross, 1939) between typically deciduous and permanent shoots, were studied. The results indicate that these shoots have apical meristems essentially similar to those of the permanent shoots (figs. 19, 20).

In summary, three distinctive types of shoot apex, with respect to the structure of the surface layer, were found in *Taxodium*, viz., apices which possess a highly organized tunica—found in permanent shoots, inter-



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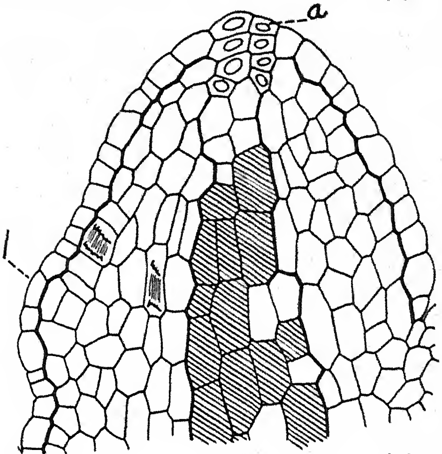

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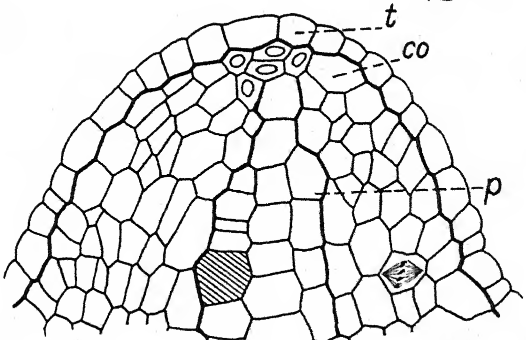

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Fig. 17. Nearly median section of shoot apex of expanding deciduous shoot; *a*, apical initials; *p*, pith initials. ×330.

Fig. 18. Median section of shoot apex of expanding deciduous shoot; *a*, apical initials; l, primordium of leaf. ×330.

Fig. 19. Nearly median longisection of shoot apex of transitional proliferating shoot. ×330.

mediate shoots, and many deciduous shoots; apices in which the continuity of the tunica is interrupted temporarily by occasional periclinal divisions —found in many deciduous shoots and possibly occasionally in permanent ones; and apices in which the continuity of the surface layer is more or less permanently interrupted by a mass of periclinally and anticlinally dividing, genetically related cells—found infrequently in deciduous shoots. These types are connected by many intergrading forms.

THE SUBAPICAL PORTION OF THE SHOOT APEX

The subapical portion of the shoot apex consists in part of a zone of central embryonic cells equivalent in position, but not in structure, to the "central mother cells" of *Ginkgo* (Foster, 1938). The subapical initials, unlike the surface cells, have a relatively uniform structure in the various shoots (figs. 13–22; Plate 2, figs. 1–3). In the deciduous shoots there are 4–8 subapical initials arranged as a cap over the initials of the pith (figs. 14, 16, 18; Plate 9, fig. 1). As a result of periclinal and anticlinal divisions, derivatives are produced which augment the pith initials and contribute laterally to the flanks of the apex respectively. The procedure probably is reduced to its simplest terms in Plate 2, figure 1, where recent subapical activity can be traced with reasonable certainty. In the apex, immediately beneath the tunica in this illustration is a group of four cells consisting of a large pith initial and three overlying smaller cells. It seems evident that these four cells constitute a genetically related group which has developed from a single mother cell by the insertion of three walls. The flanks of the corpus diverge laterally from the three smaller cells of this genetic group and ultimately differentiate into the procambial and cortical regions of the shoot. In deciduous shoots which lack a tunica (figs. 17, 18), essentially the same situation obtains with respect to the subapical initials except that the divisions tend to be somewhat oblique.

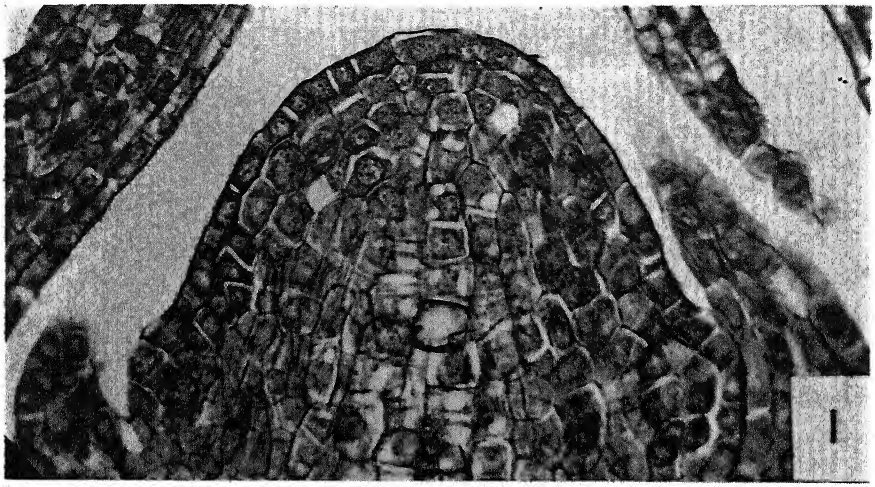
The subapical initials of the permanent shoots are arranged in several tiers, thus giving a more massive appearance to the apical meristem (fig.

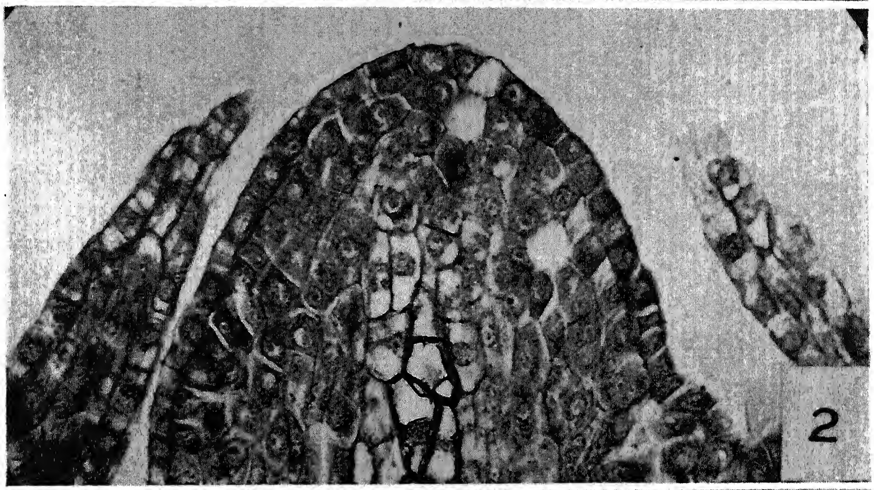
Explanation of Plate 9

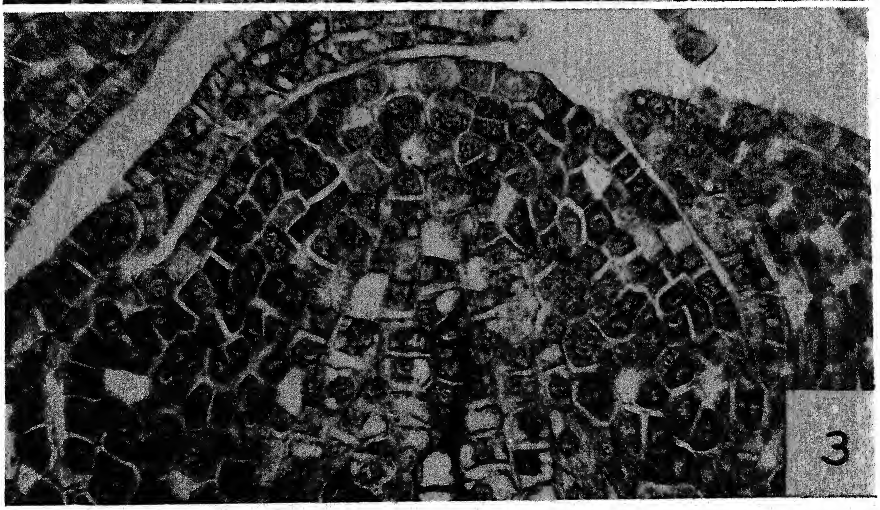
Fig. 1. Longisection of shoot apex of expanding deciduous shoot showing a clearly delimited tunica and corpus. ×330.

Fig. 2. Longisection of shoot apex of an expanding deciduous shoot showing a group of apical initials in one of which a periclinal wall has been inserted. ×330.

Fig. 3. Median longisection of shoot apex of an expanding permanent shoot showing a clearly delimited tunica and corpus—a prevailing condition in permanent shoots. ×330.







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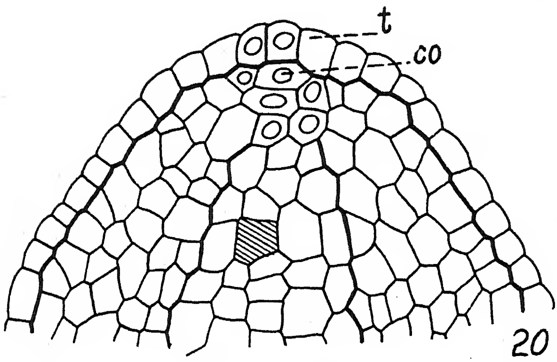
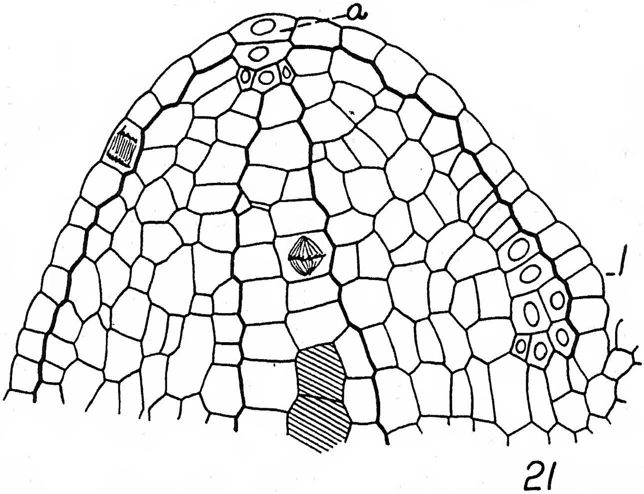




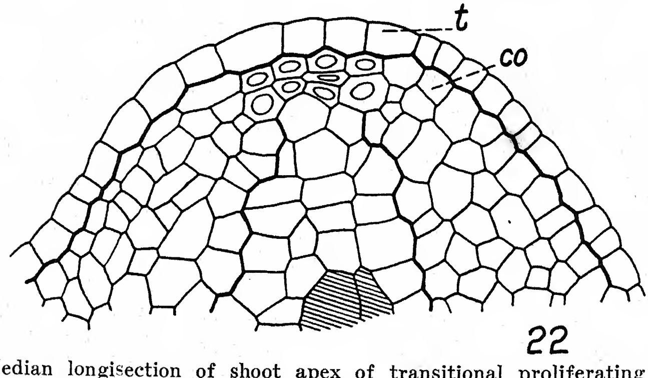


Fig. 20. Median longisection of shoot apex of transitional proliferating shoot; *t*, tunica; co, corpus. ×330.

Fig. 21. Nearly median longisection of shoot apex of expanding permanent shoot showing evidence of periclinal division in the tunica; *a*, apical initial; *l*, primordium of leaf. ×330.

Fig. 22. Median longisection of shoot apex of expanding permanent shoot illustrating prevailing condition. ×330.

22; plate 9, fig. 3). The initials divide anticlinally as well as periclinally and are similar in other respects to the subapices of the deciduous shoots.

The pith is delimited arbitrarily by a heavy line in the illustrations (figs. 14–22). The line is necessarily arbitrary because of the vague lateral limits of the older portions of the pith (Plate 9, figs. 1–3). The initials of the pith frequently extend to within two cells of the surface layer (figs. 14, 16, 18, 19; Plate 9, fig. 1). They form a "rib meristem" (Schüepp, 1926) which is continuously augmented from above by periclinal divisions in the subapical initials. The cells of the young pith are of the typically highly vacuolated type (Plate 2, figs. 1–3), common in the stem apices of many conifers (Koch, 1891; Korody, 1937).

Certain of the pith cells have densely staining materials deposited in their protoplasts, particularly in the peripheral cytoplasm. The central vacuole and the nucleus usually remain free of such deposits (Plate 9, figs. 1–3) and mitotic activity is in no way inhibited. The densely-staining cells are indicated by hatching in the text figures.

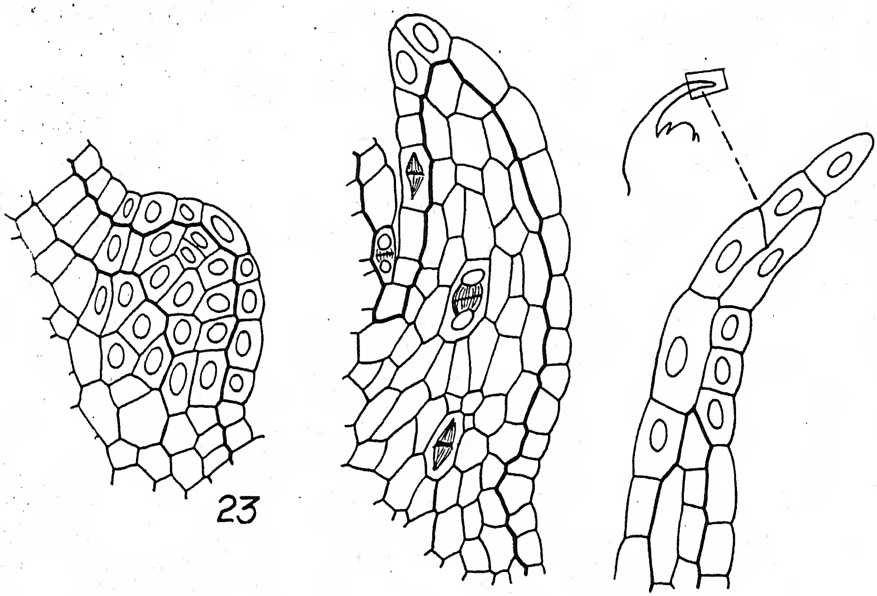
It seems evident that the subapical portion of the stem apex of *Taxodium* consists of three regions characterized by the position, size, staining reaction, and mode of division of the constituent cells, viz., the central initials; the pith initials; and the meristematic flanks, derivatives of which differentiate into procambial and cortical tissue. It further seems evident that the angiospermous condition is attained by the permanent shoots and many of the deciduous shoots of *Taxodium;* the only significant difference is that, in many angiosperms, the pith initials are differentiated at a considerably greater distance from the shoot apex (Foster, 1935; Cross, 1936, 1937b).

ORIGIN OF LEAVES

In many primitive vascular plants which lack a differentiated surface layer at the shoot apex, leaf initiation is characterized by periclinal divisions in the epidermal layer as well as in the subepidermal layers. This type of leaf initiation occurs in *Abies, Picea, Pinus* (Korody, 1937), *Lycopodium* (Härtel, 1938), and in various other gymnosperms (Strasburger, 1872). In many angiosperms (Foster, 1935; Cross, 1937b, 1938) periclinal divisions do not occur in the tunica during foliar initiation. Because *Taxodium* is regarded in this paper as being intermediate with respect to its apical meristem between the condition obtaining in primitive vascular plants and that expressed by angiosperms, it was thought ex-

pedient to include a brief description of the initiation of the leaf, with emphasis on the behavior of the epidermal layer.

Many median or nearly median sections of leaves in various stages of development were seen during the study. Leaves are initiated approximately 100μ in deciduous shoots and 80μ in permanent shoots below the shoot apex. Preliminary stages in leaf initiation involve an elongation of



23 24 25

Figs. 23, 24. Median longisections of young leaves showing contributions of epidermis and subepidermal layers during initiation. ×330.

Fig. 25. Median longisection of young leaf 350μ high showing derivation of apical portion from epidermal cells. ×330.

the cells of the subepidermal layer in a plane perpendicular to the surface of the stem. One or more of the subepidermal cells usually divides periclinally during or after elongation (figs. 16, 18, 21). Periclinal divisions were never observed in the epidermal layer, a fact which is in agreement with Karsten's (1886) brief account of foliar initiation in the seedling. Further periclinal divisions, apparently largely in the derivatives of the subepidermal layer (fig. 23), increase the size of the primordium. The epidermal layer maintains its identity and shows no indication of periclinal divisions until a height of approximately 110μ has been attained, measuring along the adaxial surface. At this stage two epidermal cells, conspicuous because of their size and distinctive shape, may be seen in

longitudinal section at the apex of the young leaf (fig. 24). These two cells maintain their identity without dividing until the leaf is nearly 150μ high. They then divide in such a manner as to form two vertical adjacent rows of cells (fig. 25). The derivatives divide anticlinally, parallel with the longitudinal axis of the leaf, and form a triangular apex two cells in thickness. Ultimately, one of the pair of dividing apical cells, usually the abaxial one, grows beyond the other (fig. 25) and forms a single-celled apex. Thus the epidermal layer contributes nothing during initiation to the internal portions of the leaf and contributes only sparingly during the later growth of the leaf.

DISCUSSION

It has been suggested by Korody (1937) and Härtel (1938) that the entire apical meristem in certain of the more primitive vascular plants is homologous with the corpus in angiosperms. This viewpoint has been criticized by Foster (1938) who regards the tunica and corpus as interdependent growth zones. In some of the deciduous shoots of *Taxodium distichum* apical meristems are found which are comparable in structure to those reported by Korody (1937) for *Abies*, *Picea*, and *Pinus*. According to Korody's interpretation, the apex of each of these deciduous shoots would consist of a corpus without a tunica. Other deciduous shoots of *Taxodium* seem to have meristems in which an incipient tunica is present. In such cases the continuity of the primitive tunica is interrupted more or less frequently by the insertion of periclinal walls, but the presence of a semi-independent surface layer is not to be doubted. Still other deciduous shoots, and probably all permanent shoots, have a tunica and corpus existing as constantly discrete histogens. Many shoot apices transitional between these three types were seen. Additional study would doubtless reveal that a much closer series could be demonstrated than that shown in figures 14–22. Again applying the principles adduced by Korody, one is forced to homologize the corpus of the permanent shoots with the entire apical meristem of certain of the deciduous shoots. Further, the corpus of one group of deciduous shoots would be homologous with the entire apical meristem of other deciduous shoots located on the same tree. In other words, the tunica, according to Korody, is a phylogenetic derivative of the corpus. The validity of such reasoning depends upon the meanings arbitrarily assigned to the words "tunica" and "corpus." As originally introduced by Schmidt (1924) these terms were used to describe differentiation in the form of zonation at the shoot apex. In my opinion

the application of Korody's interpretation does not lead to a greater understanding of the fundamental morphology of the shoot apex in vascular plants. It seems more reasonable to assume that the relatively undifferentiated shoot apex found in many gymnosperms is equivalent to the entire angiospermous shoot apex—that the tunica and corpus appear simultaneously as a result of phylogenetic zonation.

From a single branch of *Taxodium*, an evolutionary series can be arranged showing shoot apices of varying degrees of evolutionary advancement. It is of course difficult to determine in which direction the series should be read, but there is a temptation to regard as primitive those apices with undifferentiated histogens. This seems logical, especially in the light of information obtained from the study of other relatively primitive vascular plants (Korody, 1937; Härtel, 1938; Foster, 1938). Foster (1938) regards "the condition in the Abietaceae as indicative of a transitional stage in the evolution of the zonation typical of the shoot tip in angiosperms." He further suggests that "the structural pattern in *Ginkgo*" may be more primitive than the condition in the Abietaceae. It seems reasonable to interpret the condition in the deciduous twigs of *Taxodium* as more advanced than in the Abietaceae, because in this genus periclinal divisions in the surface layer of the shoot apex are restricted to the apical cells; the cells in the surface layer on the flanks of the shoot apex divide only anticlinally. The permanent shoot of *Taxodium*, with its morphologically independent tunica and corpus, may be regarded as having attained the angiospermous condition.

SUMMARY

The shoot apices of the axillary deciduous shoots and permanent shoots of *Taxodium distichum* are described. In the primordial condition the apical meristems of all shoots investigated are characterized by a clearly delimited tunica and a central corpus. This condition persists during the expansion of most of the permanent shoots and a large proportion of the deciduous shoots. Occasional periclinal divisions occur in the surface layer at the shoot apex of many deciduous shoots. In other deciduous shoots periclinal divisions in the surface layer at the shoot apex occur so frequently that the continuity of the outer layer is completely interrupted by a zone of apical initials. Derivatives of the apical initials augment the subapical portion of the apex.

The subapical portion of the shoot apex in both types of shoots consists of three meristematic regions, i.e., the subapical initials; the

meristematic flanks; and the pith initials. The subapical initials located immediately below the apex constitute a focus of meristematic activity from which the other meristematic regions diverge. The pith initials, located immediately below the subapical initials, form a "rib meristem," derivatives of which mature into pith cells. The meristematic flanks diverge laterally from the subapical initials. Derivatives of this region ultimately differentiate into the cortical and procambial tissues of the axis of the shoot.

The primordia of leaves are initiated by the radial elongation and periclinal divisions of the outer layer of the corpus. The surface layer (tunica) does not contribute to the internal tissues of the primordia during initiation.

It is suggested that the shoot apices of the various shoots of *Taxodium* constitute a developmental series which might be useful in understanding the evolution of the highly organized angiospermous apical meristem. In this series it has seemed logical to interpret as most primitive those deciduous shoots in which a group of apical initials interrupts the continuity of the tunica. This type of shoot apex is regarded as slightly more advanced than the apices of many other conifers (Koch, 1891; Korody, 1937) because periclinal divisions in the surface layer are restricted to the apex and do not extend to the flanks of the shoot tip.

The data obtained from this study do not support the theory that the shoot apex in many primitive vascular plants is homologous with the corpus in angiosperms (Korody, 1937; Härtel, 1938).

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Additions to the Flora of the Glacier Bay National Monument, Alaska, 1935-1936

William S. Cooper

Collections by W. S. Cooper, 1935

In 1931 I published in this journal a list of the seed-plants and ferns of the Glacier Bay National Monument, Alaska,[1] based on collections made in the course of three expeditions, in 1916, 1921, and 1929. A few species collected by others at various times were included. A fourth expedition took place in 1935, in collaboration with Mr. W. O. Field, Jr., during which additional collections were made; to the previous total of 232 species, 31 have been added.

The glacial history of the region, necessary to an understanding of the vegetational features, has been presented in a recent paper.[2] A brief outline of my ecological studies is provided in the paper in this journal noted above, and detailed discussion will be found in three previous publications.[3] The ecological results of the 1935 expedition are embodied in a paper just issued.[4]

The additional species collected in 1935 are listed below, with the stations where found,[5] and notes as to habitat.

Equisetum fluviatile L. Bog on foreland (57).
Agrostis exarata Trin. Pioneer. Johns Hopkins Fiord.
Calamagrostis canadensis (Michx.) Beauv. Bog meadow on foreland (57).
Deschampsia caespitosa (L.) Beauv. Beach meadow on foreland (53).
Festuca ovina brachyphylla (Schult.) Piper. Pioneer (26).
Carex aquatilis Wahl. Bog meadow on foreland (57).
Carex aurea Nutt. Pioneer on wet gravel (54).
Carex brunnescens Poir. Bog meadow on foreland (57).
Carex leptalea Wahl. Bog meadow on foreland (57).
Carex limosa L. Bog on foreland (56, 57).
Carex pyrenaica Wahl. Bare sandy outwash on foreland (57).
Carex rostrata Stokes. Bog meadow on foreland (57).

[1] The seed-plants and ferns of the Glacier Bay National Monument, Alaska, Bull. Torrey Bot. Club, **57**: 327–338. 1931.

[2] Cooper, William S. The problem of Glacier Bay, Alaska: a study of glacier variations. Geogr. Rev., **27**: 37–62. 1937.

[3] Cooper, William S. The recent ecological history of Glacier Bay, Alaska, Ecology, **4**: 93–128, 223–246, 355–365. 1923.

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[4] A fourth expedition to Glacier Bay, Alaska, Ecology, **20**: 130–155. 1939.

[5] For locations of stations see Ecology, **12**, p. 62, fig. 1, and Ecology, **20**, p. 131, fig. 1.

Carex spectabilis Dewey. Bog on foreland (56).
Carex viridula Michx. Bog meadow on foreland (57).
Eriophorum chamissonis Mey. Pioneer at edge of pond (54); bog on foreland (56).
Juncus arcticus Willd. Wet-ground pioneer (26); bog meadow on foreland (57).
Goodyera decipiens Hook. Young climax forest on foreland (57).
Rumex occidentalis Wats. Bog on foreland (56).
Ranunculus cymbalaria Pursh. Gravel shore (26).
Ranunculus repens L. Beach meadow on foreland (53).
Arabis lyrata L. Pioneer on gravel (26, 27, 54).
Drosera rotundifolia L. Bog on foreland (57).
Parnassia parviflora DC. Wet-ground pioneer (26). This collection is in habit exactly like *P. kotzebuei* Cham., which is common in the region. In floral characters, however, it corresponds closely with *P. parviflora*, not previously reported.
Saxifraga bronchialis L. Pioneer on gravel (26).
Lathyrus palustris L. Beach meadow on foreland (53).
Epilobium palustre L. Bog on foreland (56, 57).
Vaccinium oxycoccus L. Bog meadow on foreland (57).
Gentiana humilis Stev. Beach meadow on foreland (53).
Nephrophyllidium crista-galli (Menzies) Gilg. Bog on foreland (56).
Mimulus langsdorfii Donn. Stream bank on foreland. Bartlett Cove.
Taraxacum officinale Weber. Edge of alder thicket on foreland (56).

Of these 32 species added to the flora, 25 were found on the foreland east of the mouth of the bay, which is composed of glacial and glaciofluvial material associated with the recent ice maximum of 150 to 200 years ago. In 1935 for the first time a serious attempt was made to investigate the flora and vegetation of this area. Since it is close to regions long undisturbed by glaciation, the list is naturally far more extensive than that of the shores recently vacated by the ice. Particularly noteworthy is the rich vegetation of bog areas, from which 16 additional species were listed. The vegetation cover is complete, and overlies considerable bodies of peat. For all this development the maximum time available is but two centuries. It is remarkable how rapidly a rich and varied vegetation may become established upon newly formed glacial deposits, provided sources for seed and spores are close at hand.

Aside from the foreland, the region adjacent to the bay yielded but nine additional species (two appearing also on the foreland). This is due in part to comparatively thorough previous exploration, coupled with lesser emphasis upon listing and collection on the last expedition.

It seems certain, however, that invasion of recently vacated areas, relatively remote from the ice limit at its recent maximum, is still proceeding very slowly. The bulk of the vegetation is still made up of a few species. Some idea of the rate of progress may be gained from Station 26, a typical pioneer locality in 1916 with an ice-free history of 37 years. Species lists covering approximately the same area were made in 1916 and 1935. In the former year 21 species were found, in the latter 50, including 17 of those listed in 1916. Among the list of 1935 are six previously unreported from the Glacier Bay region. The remainder had already been found in other pioneer localities.

COLLECTIONS BY DAVID BRINK, 1936

In 1936 a glaciological expedition forming a part of Mr. Bradford Washburn's exploratory program spent several weeks in the vicinity of Crillon Lake on the west flank of the Fairweather Range. Mr. Russell Dow was the leader, and Mr. David Brink, then a student at the University of Minnesota, was a member of the party. Mr. Brink, although not a botanist, brought back an excellent and representative collection of the local flora. The list is worth publishing because the region in which the collection was made, being very difficult of access, had been heretofore unexplored botanically. It is a narrow strip of coastal land lying between the ocean and the lofty, ice-covered Fairweather Range, which makes an effective barrier on the east. Glaciers descend at one point to the beach and to tidewater in Lituya Bay. At several other pionts they almost reach the shore. The glacial history is in marked contrast to that of Glacier Bay on the other side of the range. Advance is the order of the day and there has been no general retreat for several decades at least. Within recent months the region between the Fairweather Range and the ocean has been added to the Glacier Bay National Monument.

A total of 87 collections yielded 65 species. Detailed comment on habitats is not possible; it may be noted, however, that the principal communities represented are alpine meadows, pioneer aggregations near glaciers, and climax spruce-hemlock forest. The list follows:

Lycopodium sitchense Rupr.
Chamaecyparis nootkatensis (Lamb.) Spach.
Picea sitchensis Carr.
Tsuga heterophylla (Raf.) Sargent
Tsuga mertensiana Carr.
Calpodium wrightii Scribner and Merrill (*Poa wrightii* Hitchc.)
Deschampsia atropurpurea (Wahl.) Scheele
Festuca ovina brachyphylla (Schult.) Piper

Phleum alpinum L.
Luzula piperi (Cov.) Jones
Streptopus amplexifolius americanus Schultes
Populus trichocarpa T. & G.
Salix sitchensis Sanson
Alnus rubra Bong.
Alnus sinuata (Regel) Rydb.
Oxyria digyna (L.) Hill
Stellaria longipes Goldie
Anemone narcissiflora L.
Caltha leptosepala DC.
Ranunculus bongardi Greene
Ranunculus cooleyae Coult. & Rose
Arabis lyrata glabra (DC.) Hopkins
Arabis pycnocarpa glabrata (T. & G.) Hopkins (*A. hirsuta,* authors)
Heuchera glabra Willd.
Leptarrhena pyrolifolia (Don) R. Br.
Ribes bracteosum Dougl.
Saxifraga bongardi Presl
Saxifraga nelsoniana Don
Tellima grandiflora (Pursh) Douglas
Aruncus sylvester Kostel. (*A. vulgaris* Raf.)
Geum calthifolium Menz.
Geum macrophyllum Willd.
Lutkea pectinata (Pursh) Kuntze
Rubus arcticus L.
Rubus spectabilis Pursh
Sorbus sitchensis Roem.
Lupinus nootkatensis Don
Viola glabella Nutt.
Viola langsdorfii Fischer
Epilobium hornemanni Reichenb.
Epilobium latifolium L.
Fatsia horrida (Sm.) B. & H.
Cornus canadensis L.
Cassiope mertensiana (Bong.) G. Don
Cassiope stelleriana (Pall.) DC. (*Harrimanella stelleriana* (Pall.) Coville
Cladothamnus pyrolaeflorus Bong.
Loiseleuria procumbens Desv.
Menziesia ferruginea Smith
Phyllodoce glanduliflora (Hook.) Coville
Vaccinium caespitosum Michx.
Vaccinium ovalifolium Smith
Vaccinum uliginosum L.
Dodecatheon pauciflorum (Durand) Greene
Primula cuneifolia Ledeb.
Gentiana calycosa Griseb.
Nephrophyllidium crista-galli (Menzies) Gilg.
Castilleja pallida subsp. *elegans* (Ostenfeld) Pennell
Mimulus langsdorfii Donn
Veronica alpina L.
Sambucus melanocarpa Gray
Valeriana sitchensis Bong.
Campanula lasiocarpa Cham. and Schlecht
Achillea borealis Bong.
Anaphalis margaritacea occidentalis Greene
Arnica latifolia Bong.
Erigeron peregrinus (Pursh) Greene
Hieracium .gracile Hook.

Determinations of the Glacier Bay materials have been checked by Dr. Paul C. Standley, except for the grasses, which were referred to Mrs. Agnes Chase. Mr. Brink's collections were checked by Dr. Julian A. Steyermark.

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Some Reactions of the Vegetation in the Towns and Cities of Nebraska to the Great Drought

Raymond J. Pool

That unusually severe drought prevailed for months at a time in the northern prairie and plains area of the United States from 1933 to 1938 has become widely known. The dependence of the people of this area upon the products of the land has become emphatically emphasized even to those most widely separated from farm problems in their social and routine contacts of daily life. The paralyzing effects of the drought greatly intensified the suffering of the people in this area, suffering that had been associated with the nation-wide depression which was well developed before crop failure and dust storms swept over the prairies. Black blizzards and cosmic winds that spread a pall of dust from the Trans-Missouri prairies to the Atlantic seaboard carried an impressive message of some of the more obvious natural conditions of the time.

The devastating influence of the drought throughout a vast territory has become best known because of its relation to the ruination of crops and the shortage of feed for livestock. The consequent failure of hundreds of small-town banks and thousands of farmers, and the intensification of unfavorable industrial and economic conditions throughout the area are other natural reactions that have attracted the attention of the nation. Much has been written concerning the effects of recurring drought upon the native and introduced plant life and crops of the region. Many biologists, conservationists, economists, and farmers have wondered if man has not seriously erred in attempting to introduce too widely the types of land utilization which have been proved sensible under more favorable and dependable climatic setups. Widespread interest in man's relationship to natural balances has been created by the disaster. At any rate we are now thoroughly aroused over the situation and tremendous efforts are being pushed by the federal government and various states to trace the causes and to find a way out of the misery. We have here an extremely complex but intriguing problem of first magnitude in the general field of ecology.

As one dry year followed another additional evidences of the destructive effects of increasing water deficiency became prominent. Crop failure was intensified, pastures became thin and poor, quick-growing, shallow-rooted weeds became prominent everywhere. Subsoil moisture was depleted to such a degree that deep-rooted native plants, and crops began to

die or failed to mature. Extremely high temperature and sweeping winds continued to rob the soil and every growing thing of their water supply to an alarming degree. Deep-rooted shrubs and trees began to show the unmistakable symptoms of severe water depletion. Insects and other organic pests took additional toll of every living plant during these troublesome years.

The plant life of our cities and towns mirrors many aspects of the severe damage that the long years of drought have produced in the fields and in the native prairies and woodlands. The most conspicuous effects are noted by the casual observer in the damage which was done to the trees of our urban communities. Many of the larger trees were either killed outright or were badly crippled during the first two or three years of the drought. As dry conditions continued and the subsoil became drier the effect upon the trees of streets, lawns, and parks became more and more prominent. Many of our people were puzzled about the matter at first, and they often sought to explain the loss of trees by reference to borers or other obvious pests. It was difficult to believe that there could not be sufficient water in the deeper soil to supply the demands of our trees, especially for trees along the streams. The trees in town were watered, and still many of them perished. The natural water balance was so severely disturbed that practically all of the older trees began to show the creeping influence of a lowering water table. Fifty per cent or more of the trees of many of our towns died. Since the largest and oldest trees were most severely involved the condition became unusually noticeable. Unsightly conditions appeared everywhere because of the dead trees. Severely pruned and pollarded cripples stood along every street. Large old trees felt the ravaging effects of severe conditions more acutely than did the smaller and younger individuals. The most of the dead trees were removed after a year or two, thus opening the lawns and parkways to the more direct influence of sun and wind. Cities installed saw mills in which logs from the stricken trees were cut into hundreds of cords of firewood and even into thousands of feet of lumber.

Observations on the effects of the protracted drought of the 1930's upon our trees have corroborated to a striking degree various conclusions which have grown from studies of such phenomena dating back to the time when the pioneers of the prairie began to plant trees here. One of these conclusions that the latest drought emphasizes is that the prairies are relatively treeless because of the natural conditions that prevail here now. The prairie represents an ecological complex that is likely to be

inimical to the life of trees and even suddenly death-dealing in its severity upon trees. The prairie is characterized positively by a broad, sweeping landscape which is dominated by grasses and their low-growing, drought-resisting associates. The prairie is also characterized negatively by the relative absence of trees.

The drought has also emphasized the reliability of our earlier judgment concerning the relative adaptability of various kinds of trees for artificial culture in the cities and towns of the prairie region. But we know now, better than ever, what kinds of trees are most likely to succeed and to survive (even when old and large) and which ones are most likely to be damaged and killed by continued dry weather. The trees have been exposed to a test during these years that has been so severe and protracted as to reveal the stability of the most drought-resistant types.

Botanists and tree specialists know that the relative position of different species in a scale of drought resistance and drought endurance is markedly influenced by the age and size of the individual tree. A citizen may feel that a certain tree, say the hackberry, is unusually good for planting under our conditions because of the fact that his hackberry lived through the drought, and that the basswood was a poor tree to use, because the latter tree on his lawn had died. But the hackberry in this instance may have been a small, young tree and the basswood a much larger, older tree. Or again, the former tree may have been growing in a spot that enjoyed much better water relations than the latter. Such common observations as the above suggest that our scale of drought resistance must be made only after a study of the behavior of the different trees of various ages and under a wide variety of environmental conditions.

Our wide study of the behavior of planted trees in the Nebraska region for forty years, including the extremely severe recent drought period, indicates that the hackberry (*Celtis occidentalis*) should be placed at the top of the list for dependability to endure and to live through long periods of severe drought. Other trees may be, and indeed are preferred, by many of our citizens, for various sensible reasons, but we are not concerned with those reasons at this time. We must understand that the "miracle," if indeed there is one at all, in the severe relationships of planted trees to the prairie complex, is not in the fact that thousands and thousands of trees have been killed by the dry weather, but that any of them have survived! The hackberry stands out as our most successful tree in this matter as we examine all features of the problems

involved. And yet, even a good many hackberry trees (especially large, old ones) perished during the years of the great drought.

The persistence of the honey locust (*Gleditsia triacanthos*) and the green ash (*Fraxinus pennsylvanica* var. *lanceolata*) has also been notable in the face of the extreme conditions of the drought. I place the former in the number two position in my list, since it unquestionably endures great extremes of desiccation (and accompanying troubles) at various age and size classes, and under the great variety of conditions in which we plant our trees. Insect troubles (particularly borers) have been prominent in the green ash.

Silver maple (*Acer saccharinum*) and the sycamore (*Platanus occidentalis*, very little *P. orientalis* and *P. acerifolia*) have also withstood the rigors of the time remarkably well. These have lived through the stress even in the form of large trees when they have occupied the most favorable sites. But the silver maple, being one of the earliest and most widely planted species, presents a miserable picture, in general, because of the damage and loss to a great many of the fine old and large trees.

The white elm (*Ulmus americana*) has also been widely planted and beautifully successful over a wide territory, but the older, finer specimens of this species have suffered severely. Many of the drought stricken elms have become extremely bristly on account of the formation of dense fringes of "sap sprouts" along the trunk and large branches. Such trees have been severely cut back and bluntly topped, a treatment that still further adds to the ugly aftermath of the drought. The red elm (*U. fulva*) has not been planted in such numbers as the white elm, but the larger trees of this species have been seriously damaged and many of them have died.

Besides the above trees, all of which are native to eastern Nebraska, many additional species have been planted in our cities and towns, along with numerous other kinds that do not occur here naturally. The native cottonwood (*Populus Sargentii*), glorious tree of the pioneers, was planted in large numbers (as single trees, in rows, and in groups) during the earlier years in the settlement of the state. Most of them had matured and practically reached the end of their life span in the cities, and had been replaced by other species before the inception of the great drought. A few magnificent old specimens of the cottonwood remained here and there and they were among the first of our trees to succumb with the onset of the drought. The loss of these monarchs of the prairie (so rich in pioneer lore) was really the prologue of the more terrible tragedy that

was to overtake other species in the years to follow. The great decorticated, white trunks and large diverging branches of those old cottonwoods were (and still are in places) ghostly evidences of a peculiarly impressive reaction to the deficiency of available soil moisture.

Many other species and varieties of broad-leaved, deciduous trees have been tried out through the years as planted intruders of the treeless grasslands. Such trees as boxelder (*Acer Negundo*), sugar maple (*Acer Saccharum*), Norway maple (*Acer platanoides*), black walnut (*Juglans nigra*), American and European linden (*Tilia glabra, T. europaea*), white poplar (*Populus alba*, inc. var. *bolleana*), Carolina poplar (*P.* sp.), white oak (*Quercus alba*), bur oak (*Q. macrocarpa*), northern red oak (*Q. borealis*), pin oak (*Q. palustris*), white ash (*Fraxinus americana*), and paper birch (*Betula papyrifera*) have been planted with variable success under widely differing conditions. Most of these have suffered severely, but it must be stated that the bur oak and even the pin oak (a lowland tree) have shown unusually fine or encouraging fortitude under the circumstances. Much of the success of the pin oak is explained by the fact that these trees were so highly regarded by the owners that they were given sufficient water from the hose to tide them over the troublesome months when other trees were being killed by the thousands. The bur oak is by nature one of the most drought-resistant of the oaks, a fact that has been reflected in its persistence through the years of ecological stress. The rapid-growing Chinese elm (*U. parvifolia*) has been widely planted in recent years as a street tree in the prairie region, and its behavior during the drought has been encouraging. We should, however, reserve our judgment with reference to the place of this tree under the conditions of periodic drought because of the fact that few of the trees had reached an age and size that would constitute a conclusive test.

We should also summarize our observations as to the behavior of planted needle-leaved evergreens in the face of the prolonged drought. The really outstanding feature of this situation is seen in the remarkably slight destruction that has befallen such trees as the native red cedar (*Juniperus virginiana*) and many of its cultivated varieties. This species has been prominent for years in the form of fine individuals in lawns and parks, and in rows as windbreaks on the farms. These trees, in general, have been damaged slightly if at all. The Austrian pine (*Pinus nigra*) and the Scots pine (*P. sylvestris*) have also survived to an encouraging degree. The Michigan white pine (*P. strobus*), sparingly planted, suf-

fered severely in most places, as did such fine trees as white spruce (*Picea glabra*), blue spruce (*P. pungens*), Norway spruce (*P. excelsa*), balsam fir (*Abies balsamea*), and white fir (*A. concolor*). The Douglas fir (*Pseudotsuga taxifolia*) has been sparingly planted in cities and towns on the prairies and it has withstood the drought to a surprising degree, but there again, the individuals of this species were commonly too young and small during the dry years to yield dependable information as to what they would do when they had become much larger. It is true that many home owners watered their evergreens sufficiently to prevent much of the damage to their trees that would surely have occurred if nature's supply of precipitation had not been supplemented.

Planted ornamental shrubs also suffered badly. The shrubs that have been most widely and successfully used as lawn plants and hedges in eastern Nebraska are the bridal wreath (*Spirea Vanhouteii*), the Amur privit (*Ligustrum amurense*), and the Japanese barberry (*Berberis Thunbergii*). Older hedges and larger isolated groups of all these were severely damaged by the drought, many of them being completely killed, or so badly disfigured as to necessitate replanting. The privet has shown a much greater degree of drought resistance than the others under a wide variety of conditions. Other broad-leaved deciduous shrubs such as goldenbells (*Forsythia suspensa*), tatarian honeysuckle (*Lonicera tatarica*), mulberry (*Morus* sp.), and the pea tree (*Caragana* sp.) were commonly killed in toto or they died back and the tops thinned to a degree that made them unsightly.

Evergreen shrubs (*Thuja* and *Juniperus*) grown as hedges have withstood the rigors of the drought to a surprisingly high degree. Such survivals have been due in certain instances to a supplementary water supply in connection with lawn watering. Broad-leaved evergreen shrubs are rarely planted in Nebraska.

Conspicuous and astounding changes also spread over the lawns, parkways, and golf courses in city and town as a result of long periods when there was little or no available moisture in the soil to depths of three to six feet, and when parching winds swept across the land. Long years of experimentation had perfected various lawn-grass mixtures that could be depended upon to make a good lawn (with more than ordinary care) in Nebraska. Bluegrass, especially Kentucky bluegrass (*Poa pratensis*) was the most significant ingredient of this lawn-grass mixture. When the soil was carefully prepared and the seeding (or sodding) well done, about all that the home owner had to do to insure the development

and maintenance of a good lawn was to apply water in sufficient quantity, keep the lawn properly fertilized and mowed, and then wage a continuous and vigorous battle against the threat of weeds. Among the more troublesome weeds in this picture were the dandelion (*Taraxacum officinale, T. erythrospermum*), water grass (*Digitaria sanguinalis*), and a host of lesser species that might become pestiferous if the necessity for eternal vigilance was overlooked. In late years the very worst weed of all, namely the bindweed (*Convolvulus arvensis*) has become prominent as a severe lawn pest.

As the drought continued year after year numerous property owners and lessees became wearied by the battle of trying to keep a good lawn against such tremendous odds. In a region where the maintenance of a lawn even under the best of natural conditions is a difficult task it is not surprising to find that many city dwellers gave up the fight and left their lawns to whatever fate nature might dictate. The common initial reaction noted in the lawns was the prompt thinning and killing of the bluegrass. When the grass was dead and brown any deep-rooted perennial and drought-resistant weed, such as the dandelion, became more and more evident. Such weeds profited at once from the complete subjugation of the lawn grasses and the removal of the competition involved. The ground often became densely covered by a choking growth of such plants. The complete invasion of the dandelion was but one example of similar situations in which the principal rôle was taken by other persistent species such as bindweed (*Convolvulus arvensis*), the puncture vine (*Tribulus terrestris*), henbit (*Lamium amplexicaule*), and others. Numerous main lawns and parkways (between sidewalk and curb) were seen in which one or the other of these ruinous species formed a complete cover over thousands of square feet.

When the bluegrass was killed in lawns where there were few or no deep-rooted perennial weeds, the bare areas were often quickly captured by such weeds as shepherd's purse (*Capsella Bursa-pastoris*), pepper grass (*Lepidium apetalum*), and penny cress (*Thlaspi arvense*), which produced a growth so dense and rank that all other invaders were repelled. Practically pure stands of these vigorous weeds were common sights in vacant lots and lawns that but a short time previously had been covered by fine bluegrass. Summer cypress (*Kochia scoparia*), lamb's quarters (*Chenopodium album*), Russian thistle (*Salsola Pestifer*), knotweed (*Polygonum aviculare*), false flax (*Camelina sativa*), milk purslane (*Euphorbia maculata*), and henbit (*Lamium amplexicaule*), were additional invaders

of weakened and bare lawns and all these became prominent during the drought. The mare's tail (*Erigeron annuus*) and the many-flowered aster (*Aster multiflorus*) were likewise common invaders and often became impressively dominant. As lawn conditions became increasingly severe many people came to welcome the presence of a dense growth of green weeds on their lawns. Such conditions were certainly to be preferred over the bare, hot, dusty and plantless expanses that one frequently noted.

One of the most interesting aspects of the sweeping succession of changes that were seen in our lawns in their reactions to the drought was the complete invasion and subjugation of many vacant lots and lawns by certain xerophytic grasses. The presence of downy chess (*Bromus tectorum*) in poorly kept or abandoned lots and lawns was a rather common condition long before the inception of the great drought in 1933. This annual weed was sometimes a real nuisance in such places, but its behavior was greatly expanded and intensified by the drought. Other annual grasses, not so often observed in this rôle before the drought, which frequently "took" lawns were certain species which are often called "poverty grasses," such as *Sporobolus neglectus*, *S. vaginiflorus*, prairie three-awn, *Aristida oligantha*, and six-weeks fescue, *Festuca octoflora*. These species invaded thousands of the bare and abandoned lawns, and large areas in parks and golf courses where they practically covered the surface to the exclusion of all other plants.

We have recorded only the more common and conspicuous reactions and changes in the plant life of our lawns and parks that have occurred during the great drought. It is already apparent, as conditions in 1938 indicate, that our people may again hope to have good lawns whenever nature supplies a more nearly normal rainfall during the critical summer months for several years in succession. But most certainly the establishment and upkeep of good lawns will remain a difficult and puzzling problem because of the aftermath of conditions (both physical and biological) spread over this vast prairie region by the great drought.

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A Flora of Eastern American Aspect in the Miocene of Idaho*

Helen V. Smith

(with plates 10–13)

A preliminary study of a fossil flora from Thorn Creek, Idaho, shows that the aspect of the flora is typically modern and immediately suggests the climax deciduous forest of the eastern United States. There are three important floristic elements and one minor one, namely (1) those species whose nearest living equivalents now grow in eastern America, (2) those now represented by living allies in the flora of the humid Pacific coast region, (3) those whose modern representatives are found in the high mountains of the West, and (4) a smaller number that have modern living equivalents in the Southwest. The eastern American element is so distinctive and interesting that the most characteristic species of it are published here in advance of a comprehensive report on the flora.

Thorn Creek, a mountain stream flowing west from Thorn Creek Mountain empties into Moore Creek, a tributary of the Boise River, at an elevation of about 3500 feet, approximately ten miles south of Idaho City, and about twenty miles northeast of Boise, Idaho. The fossil bearing beds from which the material for this study was obtained are exposed in a road cut on the south side of the valley. The matrix is a very fine grained, light colored volcanic ash in which the specimens are found unequally distributed. The preservation of the impressions is excellent and the finest details of venation can be made out readily with the aid of a lens. About three thousand specimens were examined, of which one-third were retained for laboratory study.

The following is a list of the Thorn Creek species that have as their nearest living equivalents species now occurring in the eastern United States.

Fossil species	*Living species*
Betula idahoensis H. V. Smith	*B. lenta* L.
Carpinus sp.	*C. caroliniana* Walt.
Celastrus sp.	*C. scandens* L. (?)
Fagus washoensis LaMotte	*F. grandifolia* Ehrh.
Fraxinus sp.	*F. quadrangulata* Michx. (?)
Magnolia oregoniana Chaney	*M. virginiana* L.
Populus washoensis R. W. Brown	*P. grandidentata* Michx.

* Papers from the Department of Botany and of the Botanical Gardens of the University of Michigan, No. 692.

Pteris calabazensis Dorf	*P. aquilina* L.
Quercus Eoprinus H. V. Smith	*Q. prinus* L.
Quercus Maccannii Berry	*Q. bicolor* Willd.
Quercus Merriami Knowlt.	*Q. rubra* L.
Rhododendron idahoensis H. V. Smith	*R. maximum* L.
Salix Schimperi Lesq.	*S. cordata* Muhl.
Ulmus paucidentata H. V. Smith	*U. alata* Michx. (?)

Of the species in the above list *Pteris calabazensis* and *Salix Schimperi* have as their living equivalents species which are not confined to the eastern United States. *P. aquilina* is one of the most widely distributed plants known. *Salix cordata* is also found in the Rocky Mountains and Pacific coast states.

In addition to the recorded species, there are a number of maple leaves that are very much like *Acer rubrum* L. They are not included in the list because of their equally close similarity with *A. glabrum* var. *Douglasii* (Hook.) Dippel of the west. *Quercus pseudolyrata* Lesq. is quite abundant and is probably about as close to certain eastern oaks as it is to the California species, *Q. Kelloggii* Newb., which is now usually considered to be its living equivalent.

Three species are represented only by fruits or bracts and will not be named at present because more material is to be collected and leaf impressions of those species may be encountered. *Fraxinus* is represented by several samaras, but the *Celastrus* and *Carpinus* are each represented by a single specimen and its counterpart.

Quercus and *Fagus* are the most important genera in point of abundance. *Quercus Eoprinus*, a typical chestnut oak of Appalachian aspect, is represented by more material than any other species. *Quercus* no longer occurs in southern Idaho, but is found in Oregon west of the Cascade Mountains and in California. Chestnut-leaved oaks no longer grow in the west. *Quercus* is a large genus with several hundred described species which inhabit the temperate regions of the Northern Hemisphere and medium altitudes in the tropics. In the Americas it ranges as far south as the mountains of Colombia; in Asia it extends south to the Indian Archipelago. *Fagus* is second only to *Quercus* in number of specimens. All of the material collected to date at Thorn Creek can be assigned to a single species. Of the eight recognized living species only one is now found in America. This and the fossil form are very much alike as to leaves, burs, and nuts. The living species is widely distributed in the

eastern United States in rich uplands, and on the bottomlands of streams and along the borders of swamps. One species is found over a great part of Europe. The others are found in the temperate region of eastern Asia and in the Caucasus. If the Appalachian flora is, as botanists believe, a relatively unmodified vestige of vegetation which was much more widely distributed during the Miocene, it is quite in accordance with expectation to find a single beech of eastern aspect in the western Miocene.

SYSTEMATIC DESCRIPTIONS

PTERIS CALABAZENSIS Dorf
Plate 12, fig. 2

Pteris calabazensis Dorf, Carnegie Inst. Wash. Pub. 412: 67, pl. 5, figs. 1, 2, 1930.

A single small fragment including about eight pinnules is the only fern so far discovered at Thorn Creek. There are no sori present so a convincing generic determination cannot be made. However, the fossil seems to be very similar to *Pteris* (*Pteridium*) *aquilina* L. It can be duplicated in size, shape and venation on certain fronds of this variable living species. Dorf's specimens from the Pliocene of California are likewise similar and are also very much like the Thorn Creek specimen. The fern fragment from Salmon, Idaho, figured by Brown (2) is probably also this species. It is also possible that *Dryopteris idahonensis* Knowlt. described from Montour, Idaho, is the same.

The common brake is of world-wide distribution. It is common in Canada and in the northern half of the United States where it grows in woods and open sandy places. In the humid Northwest it grows luxuriantly and attains considerable size. In drier habitats it is smaller. It is often associated with aspens and is found in open pine forests in the lower mountains of Idaho.

POPULUS WASHOENSIS R. W. Brown
Plate 10, fig. 1

Populus washoensis R. W. Brown, Jour. Wash. Acad. Sci. 27: 12, 516, 1937.

Populus Lindgreni Knowlt. LaMotte, Carnegie Inst. Wash. Pub.: 455; 115, pl. 4, fig. 1, 1936.

P. washoensis was first found in the Upper Cedarville formation of Nevada and illustrated as *P. Lindgreni* Knowlt. Since there are

several good specimens in the Thorn Creek collection and no description of the species has been previously published, one is included here.

Leaves firm, very thin, orbicular, sometimes broader than long; average length 5 cm., average width 5.3 cm.; margin irregularly coarsely crenate-dentate, teeth forward pointing, not entered by a prominent vein; apex abruptly short acuminate; base broad, often slightly cuneate; midrib fairly firm below, tapering, weak above, often curved at the point of origin of the secondaries; secondaries 4 or 5 pairs, the lowest giving off 2–4 abaxial tertiaries; secondaries somewhat irregular, often forking, ending in fine nervilles before reaching the margin; tertiaries fine, forming very irregular to almost percurrent arches between the secondaries; finer venation distinct, forming a coarse irregular or often quadrangular reticulum.

This species is characterized by the very thin texture of the blade, the coarse irregular teeth and distinct ultimate venation. It is very similar to *P. grandidentata* Michx. (Plate 10, fig. 3) which occurs from New Brunswick southward as far as the Great Smoky Mountains of Tennessee and North Carolina and as far west as eastern Minnesota, Iowa and Illinois. It usually grows on sandy slopes and stream banks and may be associated with conifers or such broad-leaved trees as maples, oaks, and service berries.

Salix Schimperi Lesq.

Salix Schimperi Lesquereux, U. S. Nat. Mus. Proc. 11: 21, pl. 8, fig. 5, 1888.

Juglans hesperia Knowlton, U. S. Geol. Surv. Eighteenth Ann. Rept. pt. 3: 723, pl. 9, fig. 8, 1898.

A large number of specimens referable to this species were found at Thorn Creek. It is characterized by the round or cordate base, numerous secondaries and very stout midrib. It was described from a single well preserved specimen from Cherry Creek, Wasco County, Oregon.

S. inquirenda Knowlt. a well known Miocene species first described from the Latah near Spokane, Washington, appears to be very similar,

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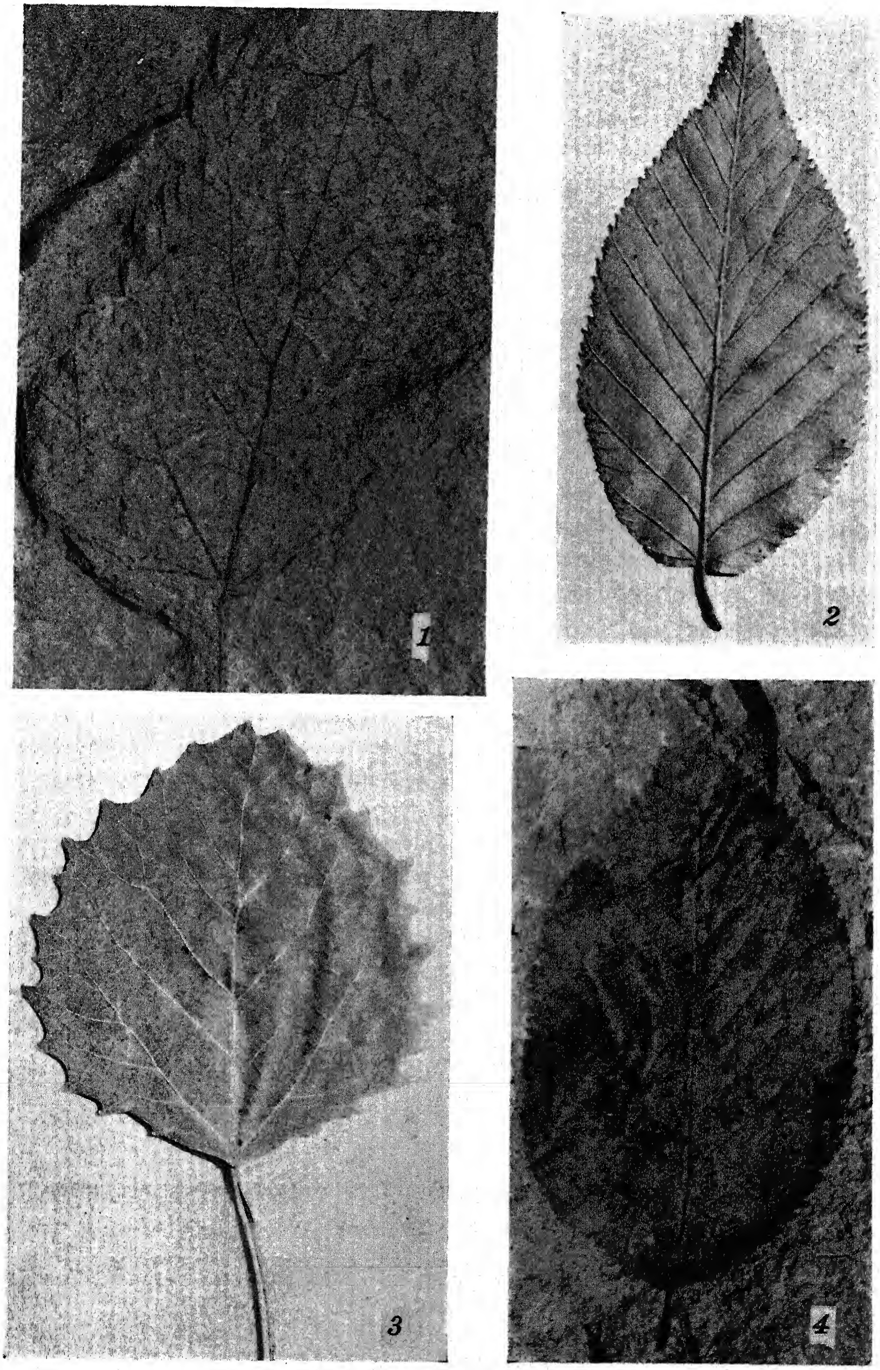
Explanation of Plate 10

Fig. 1. *Populus washoensis* R. W. Brown.

Fig. 2. *Betula lenta* L. Specimen in Herb. Univ. Mich., from Linville, N. C., for comparison with *Betula idahoensis*.

Fig. 3. *Populus grandidentata* Michx. Specimen in Herb. Univ. Mich., from St. Clair County, Mich., for comparison with *P. washoensis*.

Fig. 4. *Betula idahoensis* H. V. Smith. Type, Mus. Paleon., Univ. Mich., No. 18696.



SMITH: MIOCENE OF IDAHO

so much so that it is difficult to distinguish between them. The principal differences seem to be the usual occurrence of a cordate or rounded base and stout midrib in *S. Schimperi.*

Among living willows these leaves are similar to those of *S. cordata* Muhl., the heart-leaved willow. This is a shrubby species found growing in wet ground from New Brunswick to Virginia, Colorado, California, and British Columbia.

Betula idahoensis n. sp.
Plate 10, fig. 4

Leaf membranaceous, 6.4 cm. long, 3.5 cm. wide, broadly oblong-ovate, narrowed rather abruptly to an acuminate apex and with a broadly cuneate slightly asymmetric base; margin regularly simply serrate except just at the base where it is entire; teeth small, acute, forward pointing, those teeth entered directly by the secondaries the strongest, the 1–3 teeth between the secondaries slightly less prominent but also sharply pointed and each entered by a small, rather weak, abaxial vein; midrib not strong; secondaries about 14 pairs, alternate or occasionally almost subopposite, the lowest pair very weak, arising at the top of the petiole and extending just within the margin for a short distance; the next two pairs arising at a very acute angle and immediately curving outward, those in the midportion of the blade arising at angles of 35–40°, subparallle, straight or curving slightly, terminating in the marginal teeth, sometimes with 1–3 abaxial branches terminating in the teeth; tertiary venation obscure, consisting of very fine irregular percurrent veins; no ultimate venation visible; petiole stout, 6 mm long.

Bract of catkin three lobed, lobes of approximately equal size; lateral lobes divergent, length 6 mm., width 9 mm.

Nut small, obovate, 1 mm. wide, 2 mm. long, terminated by two minute divergent stigmas, surrounded by a membranous wing except at the stigma end, wing widest just below the origin of the stigmas, overall width at widest point 4 mm. Leaf, Mus. Paleon., Univ. Mich., type, no. 18696.

This beautifully preserved leaf is the only one of its kind in the collection. It undoubtedly belongs to the Betulaceae and a study of all available material of that family indicated its affinities with *Alnus* or *Betula*. Among species of *Alnus* it bears some resemblance to leaves of *Alnus sinuata* Ryd., but differs from the latter in the lack of short

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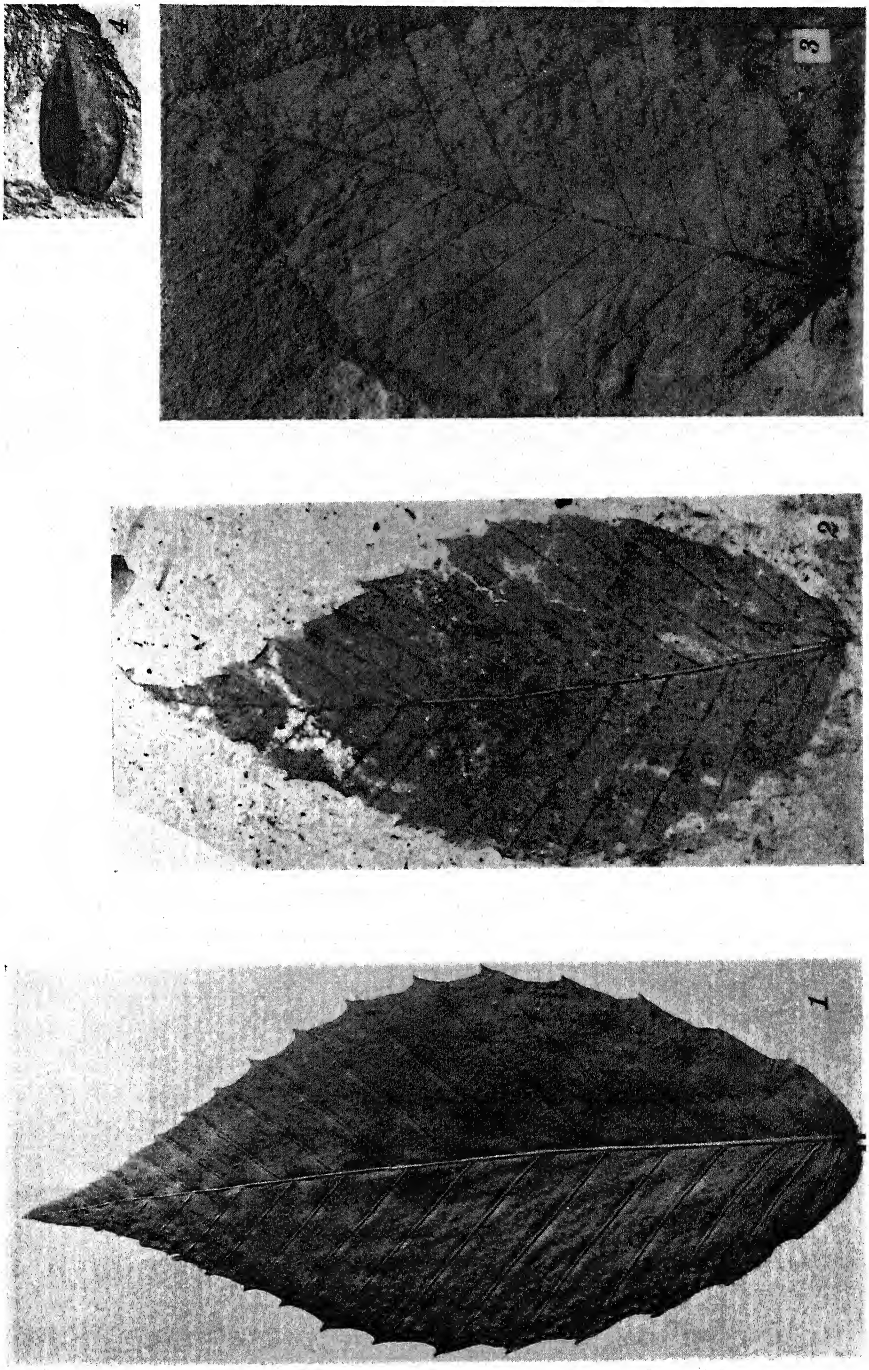
Explanation of Plate 11

Fig. 1. *Fagus grandifolia* Ehrh. Specimen in Herb. Univ. Mich., from Warren Woods, Berrien County, Mich., for comparison with *F. washoensis*.

Figs. 2, 3, 4. *Fagus washoensis*. Fig. 4, nut, $\times 1\frac{1}{2}$.



SMITH: MIOCENE OF IDAHO

lateral lobes terminating each secondary vein. *Alnus*, therefore, seems to be eliminated as a possibility. *Carpinus* and *Ostrya* are usually conspicuously unequally or doubly serrate and thus unlike the fossil. *Betula lenta* L. (Plate 10, fig. 2) the black or cherry birch of northeastern United States and the Alleghany region has leaves, bracts and seeds which very closely resemble the fossils. In fact certain leaves of the living species are almost exact duplicates of the fossil leaf.

Carpinus sp.

A single bract and its counterpart are the only specimens referable to this genus. In general shape and venation as well as in the strong marginal teeth they are similar to the involucres of *C. caroliniana* Walt. The rather narrow and quite elongated middle lobe is more suggestive of *C. Betulus* L. It is unfortunate and rather surprising that there are no leaves of *Carpinus* in the material obtained from Thorn Creek thus far.

C. caroliniana, the blue beech or hornbeam, is common in the eastern and southern United States. In the mountains of southern Mexico and Central America it is represented by *C. caroliniana* var. *tropicalis*. It reaches its maximum growth on the western slopes of the southern Alleghany Mountains and in southern Arkansas and eastern Texas.

Fagus washoensis LaMotte

Plate 11, figs. 2, 3, 4; Plate 13, figs. 5, 7, 9

Fagus washoensis LaMotte, Carnegie Inst. Wash. Pub. 455: 119, pl. 8, figs. 2, 3, 5, 1936.

Leaves of this species constitute an important element of the Thorn Creek flora. A single bur and a well preserved impression of a nut were also found. *Fagus* is not found in western North America at the present time but the single American species is abundant in the deciduous climax forest of eastern North America where it ranges as far west as Minnesota. It grows best in a deep, rich, well-drained loam, but is also found on a great variety of soils and reaches its best development on the bottom lands of streams in regions where the rainfall is 35–40 inches annually. The existing species of *Fagus* are confined to the North Temperate zone.

Of the two well described and figured species of *Fagus* from the Tertiary of the West the specimens at hand are more like those referred to *F. washoensis* although the distinction between that species and *F. paci-*

fica Chaney from Crooked River, Oregon, is not entirely clear. The Thorn Creek specimens closely resemble those figured by Berry (1) as *F. pacifica* (pl. 19, 20), and later referred to *F. washoensis* by LaMotte. It is because of LaMotte's disposition of Berry's specimens rather than my ability to distinguish two species that this identification of the Thorn Creek material is made. *F. washoensis* has also been reported from Tipton and Austin, Oregon, from the Upper Cedarville formation at 49 Camp, Nevada, and Pit River, California. The larger specimens from Thorn Creek, some of which are indistinguishable from those figured by Berry and referred to above, are very well preserved and show the nature of the margin and venation extremely well. The description of *F. washoensis* indicates that there are usually 15 or more pairs of secondaries although that number is not visible in the photographs of the specimens from Upper Cedarville formation nor are that many common in the Thorn Creek specimens. The teeth in most of the specimens are well marked and the margin should be considered to be distantly and coarsely serrate. The resemblance to *F. grandifolia* Ehrh. (Plate 11, fig. 1) is marked. The margin with strong teeth is unlike that of the figured specimens of *F. longipetiolata* Seeman with which LaMotte compared his specimens. This latter species has the margin undulate or curved in at the end of the secondaries. It is questionable where the differences between *F. pacifica* and *F. washoensis* are significant enough to distinguish two species.

Quercus Eoprinus n. sp.

Plate 12, figs. 3, 4

Leaves membranaceous but firm, 4–10 cm. long, 2.5–5.5 cm. wide, obovate or occasionally broadly elliptic; widest at the middle and narrowed abruptly to the wedge-shaped base which is usually slightly asymmetrical; apex acute; margin coarsely crenate-dentate; teeth triangular, somewhat rounded or acute and usually pointing forward, the upper teeth the smallest and most crowded, those about the middle of the blade the largest; sinuses between the teeth shallow, broad and rounded; midrib quite stout below, becoming very fine and often flexuous above; secondaries usually 11 to 14 pairs, subparallel, close together in the upper third of blade, arising from the midrib at angles of 25–50°, straight, tending to be opposite near the base and apex and alternate between, not forking, ending in the teeth or the lowest pair or two ending in the undulations of the margin; tertiaries very fine, close-set, percurrent, those near the margin not perpendicular to the midrib; ultimate venation a very fine reticulum. Type, Mus. Paleon., Univ. of Mich., no. 18697.

This fine species is obviously similar to the chestnut oaks of the Atlantic region of the United States. These oaks are characterized in part by their lanceolate or usually obovate coarsely sinuate-toothed leaves. Among the living species studied a close resemblance was found between the fossil leaves and *Q. Muehlenbergii* Engelm., *Q. prinoides* Willd. and *Q. Prinus* Auct. (non L.) = *Q. montana* Willd. fide Sargent. All three species differ from the Thorn Creek material in being larger-leaved, and *Q. Muehlenbergii* tends to have the leaves narrowly elliptic-ovate with rather pointed teeth. *Q. prinoides*, the chinqua pin oak, has fewer, coarser teeth which are spaced farther apart than those of the fossil; its leaves are often elliptic instead of obovate. The greatest similarity is found with *Q. Prinus* Auct. (Plate 12, fig. 1). This common chestnut oak grows on hillsides and high rocky banks of streams. It is found from New England along the coast to Delaware, and southward along the Appalachian Mountains to Georgia. It extends westward to western New York state, southern Ohio and southern Indiana to central Tennessee and Kentucky. It reaches its largest size and is most abundant along the banks of the lower Hudson River and on the Appalachian Mountains. In the Great Smoky Mountains it often forms a large part of the forest and may reach elevations of 4000 to 5000 feet.

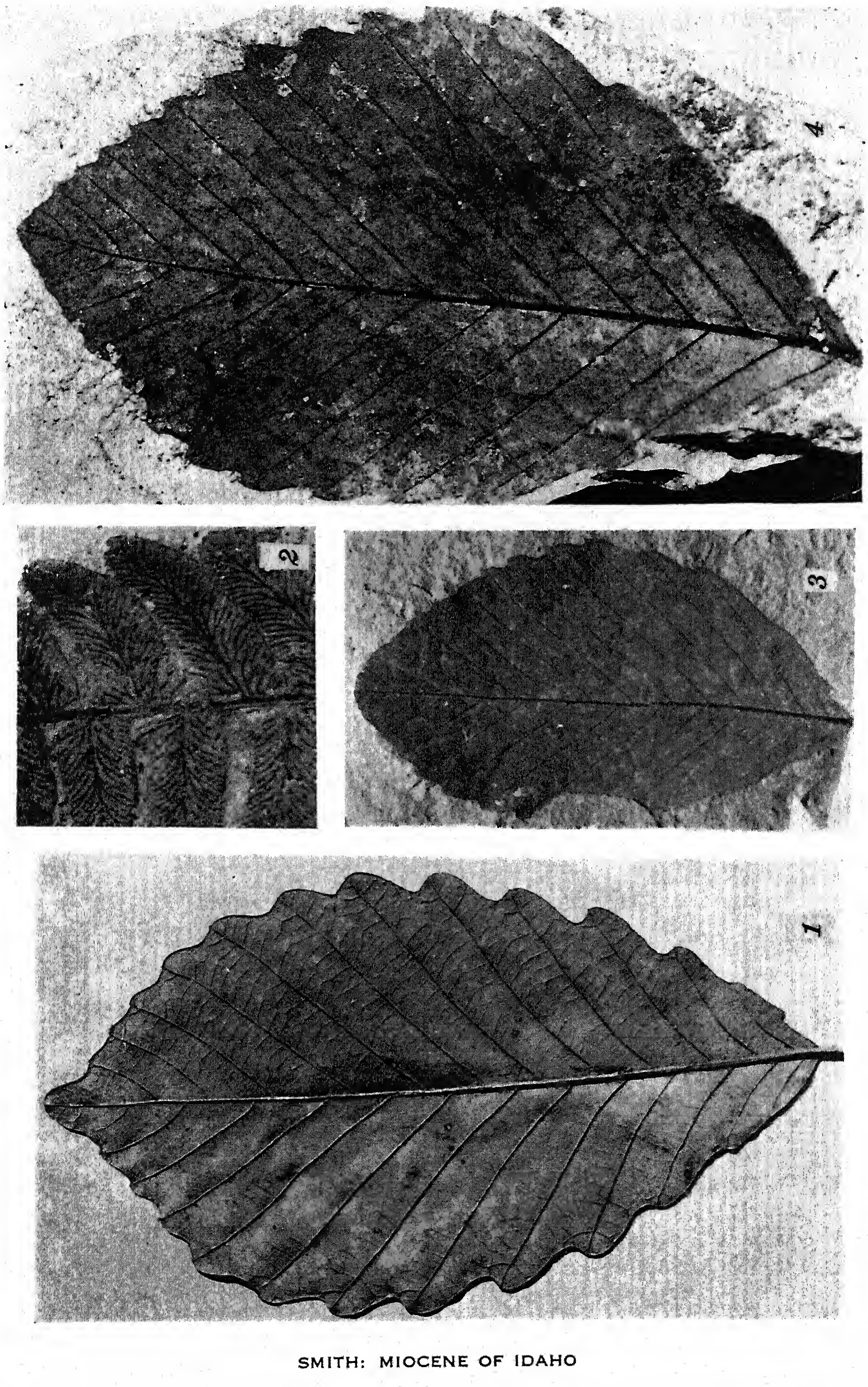
Quercus Maccanni Berry, described from the Grand Coulee and found also at Thorn Creek, is somewhat similar. Its leaves are generally coarser, with fewer secondaries, a stronger midrib, a wider angle formed by the secondaries and the midrib, and coarser tertiary venation. *Quercus spokanensis* var. *gracilis* Berry from southeast of Montour, Gem County, Idaho, is strikingly similar and may be the same species as the Thorn Creek specimens. I do not believe that this nominal variety is similar enough to *Q. spokanensis* to be included with the latter. There is also some doubt as to whether *Q. spokanensis* is even a *Quercus*. It was described from a fragmentary specimen that Brown (3) believes should be referred to *Castanea*. The smaller leaves somewhat resemble the Miocene *Q. Applegatei* Knowlt. found near Ashland, Oregon.

Explanation of Plate 12

Fig. 1. *Quercus Prinus* L. Specimen in Herb. Univ. Mich., from Sheffield, Ala., for comparison with *Q. Eoprinus*.

Fig. 2. *Pteris calabazensis* Dorf. ×3.

Figs. 3, 4. *Quercus Eoprinus* H. V. Smith. Fig. 4, type, Mus. Paleon., Univ. Mich., No. 18697.



SMITH: MIOCENE OF IDAHO

Quercus Merriami Knowlt.
Plate 13, fig. 8

Quercus Merriami Knowlton, see Brown U. S. Geol. Surv. Prof. Paper 186: 172, 1936, for synonymy.

Since *Quercus ursina* Knowlt. and *Q. Merriami* Knowlt. are considered (as suggested by Brown) to be synonyms of the same species, a new description including both of these forms is given.

Leaves subcoriaceous, firm; ovate elliptic or slightly obovate to broadly lanceolate in outline; lobed, the lobes tapering rather abruptly to the pointed apex, sometimes with one or two sharp teeth on each of the principal lobes in the larger leaves; lobes 2 to 4 pairs, at times unequal in number on the two sides of the blade, alternate or subopposite, deltoid; sinuses moderately wide, decidedly oblique; midrib moderately strong, sinuous, tapering; principal secondaries alternate, the same number as the lobes and terminating in their apices, at times forking to give off branches to the lateral teeth, arising obliquely at an angle of 25 to 45°; intermediate secondaries few, weak, apparently craspedodrome; tertiaries few, fine, somewhat irregular; ultimate venation obscure; apex of leaf acute, at times sparsely dentate, base cuneate to rounded-truncate; petiole rather long (over 1.5 cm.) and slender; length of leaf 2.5–15 cm. (estimated) and width 1.4–6 cm. between tips of lobes.

Q. Merriami as here interpreted is characterized by being deeply obliquely lobed, the lobes tapering, triangular, and frequently with a single tooth.

A study of living species shows some similarity (especially of the smaller leaves) with *Q. ilicifolia* Wang., the bear oak or scrub oak of dry sandy barrens and rocky hillsides on the eastern slope of the Appalachian Mountains and along the New England coast. Still closer is *Q. rubra* L. (Auct., non Sargent) among the many leaf types of which most specimens of *Q. Merriami* can be duplicated. The red oak is very common and is found from Nova Scotia southward in the Appalachians and west to Minnesota, eastern Kansas and Oklahoma. In the Appa-

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Explanation of Plate 13

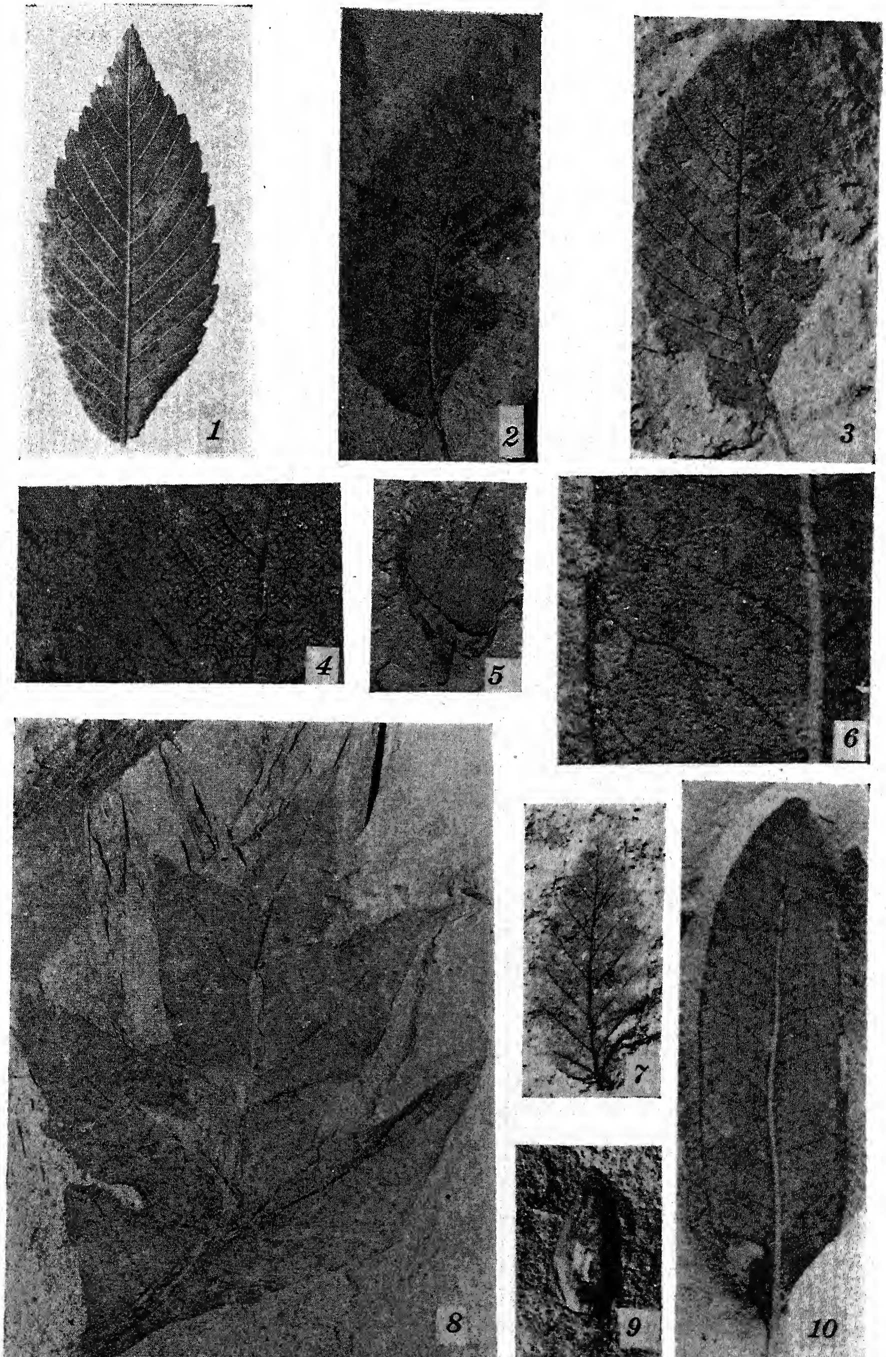
Fig. 1. *Ulmus alata* Michx. Specimen in Herb. Univ. Mich., from Swain County, N. C., for comparison with *Ulmus paucidentata.*

Figs. 2, 3, 4. *Ulmus paucidentata* H. V. Smith. Fig. 2, type, Mus. Paleon., Univ. Mich., No. 20016. Fig. 4, a portion of leaf in fig. 2, ×3.

Figs. 5, 7, 9. *Fagus washoensis*. Fig. 5, bur, ×1½. Fig. 9, a bud scale, ×1½.

Figs. 6, 10. *Rhododendron idahoensis* H. V. Smith. Fig. 6, a portion of leaf shown in fig. 10, ×3, to show venation. Fig. 10, type, Mus. Paleon., Univ. Mich., No. 20018.

Fig. 8. *Quercus Merriami* Knowlt.



SMITH: MIOCENE OF IDAHO

lachians of North Carolina it may reach elevations of 4000 feet. It is one of the largest and most widely distributed trees of the northern states.

Q. Merriami was described from the Mascall flora at Van Horn's Ranch in the John Day Basin of Oregon, and has since been reported from the Latah at Spokane and the Grand Coulee, Washington.

Quercus Maccanni Berry

Quercus Maccanni Berry, U. S. Geol. Surv. Prof. Paper 170: 36, pl. 11, figs. 5, 6, 1931.

These leaves representing a species of chestnut-leaved oak were described from the Latah flora of the Grand Coulee, Washington, and apparently have not been reported from any other locality. The coarse oblique rounded teeth are often slightly irregular in spacing and size and begin a short distance above the base which is cuneately narrowed to the rounded petiole insertion. The sinuses are rounded and oblique, the midrib strong, the secondaries thick and prominent. The percurrent tertiaries are usually 2–3 mm. apart and almost perpendicular to the secondaries.

The leaves of this species possess characters in common with those of the swamp white oak, *Q. bicolor* Willd. This oak inhabits low borders of streams and swamps from southern Maine west through southern Ontario and central Michigan south to the Ohio River and southeastern Nebraska. It extends south along the Alleghanies to northern Georgia and east of the mountains as far south as the District of Columbia. It grows with maples, sour gum, other oaks, and ashes. It is nowhere abundant but is most common and attains its largest size in western New York and northern Ohio.

Ulmus paucidentata n. sp.

Plate 13, figs. 2, 3, 4

Leaves membranaceous, straight or curved, narrowly ovate-elliptic 2.5–5 cm. long, 1–1.8 cm. wide, gradually narrowing to an acute, somewhat attenuate apex; base narrowly cuneate on one side, rounded on the other, or the small leaves are apparently rounded on both sides; margin obscurely doubly dentate, the teeth entered by the veins being quite large, obtusish, subascending, with one or two minute teeth on the basal side, or entire; midrib moderately stout, straight or curved; secondaries straight, subparallel, terminating in the coarse teeth, 10–13 pairs on the rounded side, 9–11 pairs on the cuneate, arising on the cuneate side at angles of 37–43°, and on the other at angles of 45–50°;

no distinct tertiaries, ultimate venation rather finely reticulate; petiole curved, at least 1 cm. long. Type, Mus. Paleon., Univ. Mich., no. 20016.

The small size, asymmetric base and obtuse teeth characterize this species. Most species of *Ulmus* have larger leaves but the following were found to have leaves that are sometimes the same size of those of the fossil species: *U. parvifolia* Jacq., *U. crassifolia* Nutt., *U. pumila* L., and *U. alata* Michx. None was found to be very similar to the fossil species, but all had certain characteristics in common with it.

U. parvifolia, the Chinese elm of China, Korea, and Japan, differs in that the leaves are usually widest above the middle, less cuneate on the narrow side, with the teeth more pointed and spreading rather than ascending, with no small secondary teeth and a less attenuate apex. *U. crassifolia*, the common cedar elm of Texas, is subcoriaceous, round-elliptic or nearly oblong and with veins less regularly spaced. The secondaries are forked more frequently and the margin may or may not be doubly dentate. The teeth are smaller and less prominent. *U. alata* is quite similar to the Thorn Creek species in size and appearance of the teeth (Plate 13, fig. 1). It differs in its more conspicuous and more numerous accessory teeth and in being more symmetrical at the base. *U. pumila* is also somewhat similar. Its leaves are small, not very asymmetric, but rather narrowly ovate. They are usually but not always doubly serrate and occasionally show forking of the secondaries. This is the dwarf Asiatic elm native to northern China, eastern Siberia and Turkestan. Among these elms, *U. alata* seems to be the most similar to the fossil species. The wahoo or winged elm is native from Virginia south to Florida, west Illinois, Arkansas and Texas.

Two small-leaved Tertiary species of *Ulmus* have been described. Both differ significantly from the Thorn Creek species. *U. Moorei* Chaney & Elias differs in having almost orbicular leaves with a broadly cuneate or somewhat cordate nearly symmetric base, fewer secondaries and a thicker texture. The leaves of *U. Brownelli* Lesq. are widest below the middle, with teeth abruptly narrowed to form a sharp tip, pointing outward in the basal portion and upward in the apical portion.

U. Tanneri Chaney from Eagle Creek, Oregon, shows the greatest likeness to the Thorn Creek leaves. It is however, based upon leaves that are less unequal at the base with more prominent accessory teeth and a more obtuse apex.

Only the two faces of a single specimen of an elm fruit have been found. Among living species this fruit appears to be practically identical

with the winged fruits of *U. racemosa* Thomas. The cork elm is widely distributed in north-central United States from New York to Nebraska and from southern Ontario to central Tennessee. It usually grows on dry gravelly uplands, along river cliffs or on rocky slopes.

It is quite possible that this fruit belongs to *U. paucidentata*, but no certain assignment to that species can be made until the leaves and fruits have been found more than once in association, or until sufficient collecting has been done to give reasonable assurance that the florula had only one elm species.

MAGNOLIA OREGONIANA Chaney

Magnolia oregoniana Chaney, Contr. Walker Mus. 2, no. 5: 173, pl. 15, fig. 1, 1920.

Leaf coriaceous, ovate-elliptic, about 7 cm. long, 3 cm. wide, margin entire, base round-cuneate, uneven. Except for its somewhat smaller size this single specimen is like that figured by Chaney from Eagle Creek. Its nearest living equivalent would seem to be *Magnolia virginiana* L. The sweet bay or swamp laurel occurs from Massachusetts and Long Island southward in the coastal plain to Texas. In habit it may be a small tree, but in its northern range it usually occurs as a shrub. As suggested by its common name, it usually grows in swampy places, being found along the borders of pine-barren ponds and in shallow swamps.

CELASTRUS (?) sp.

This genus is somewhat doubtfully represented by a single specimen of a three valved fruit. It bears a striking resemblance to the fruits of *C. scandens* L. Since no leaves referable to this genus have as yet been found, a description of the species is withheld.

Celastrus scandens is found throughout the eastern United States and extends as far west as New Mexico. The other species in the genus are found principally in the mountainous regions of India and China and extend to Japan, Malaya and Australia.

Rhododendron idahoensis n. sp.

Plate 13, figs. 6, 10

Leaf narrowly oblong, narrowing in the upper fourth to the acute apex and more abruptly in the basal region to the cuneate, slightly uneven base; length of best preserved specimen 5.8 cm., width 1.6 cm., width of others

up to 2.7 cm., length unknown; margin entire, slightly undulate; midrib stout, crooked; secondaries about 15 pairs, forking well within the margin to form loops with the forks from adjacent secondaries, secondaries not parallel, arising irregularly at angles of 45–65°; no tertiary venation; ultimate venation a fine obscure reticulum; surface on some specimens punctate; petiole stout, length unknown but at least .5 cm. Type, Mus. Paleon., Univ. Mich., no. 20018.

The character of the obscure venation is very similar to that of *Rhododendron maximum* L., the great laurel of the northeastern United States and Appalachian region. The fossil leaves are much smaller and thinner. *R. maximum* is a tree-like shrub that often forms large almost impenetrable thickets along streams and in wet ground in the southern Appalachians. It ranges up to about 4000 feet elevation.

FRAXINUS sp.

Several small samaras with obscure seeds were found. Except for their smaller size they resemble those of *F. quadrangulata* Michx. The latter is found in rich woods from Ontario to Michigan and Minnesota and to Alabama and Arkansas. No leaf impressions referable to *Fraxinus* have as yet been found in the Thorn Creek locality.

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Peat Formation in the Carolina Bays

Murray F. Buell

(with one figure)

On the coastal plain of North and South Carolina there are a large number of shallow, elliptical depressions, the long axis of each of them being oriented south approximately forty-six degrees east. These are commonly known as the Carolina Bays. Melton and Schriever (1933) described them and suggested a meteorite origin. Further evidence substantiating this hypothesis has been accumulated by Prouty (1935) in his magnetometer surveys. All the phenomena described by these men seem to be adequately explained only by the meteorite hypothesis. Two dissenting interpretations, however, have been presented. C. Wythe Cooke (1934) has ascribed their origin to wind action and water currents in coastal lagoons. Douglas Johnson (1937), on the other hand, has proposed an hypothesis of complex origin which involves artesian, solution, lacustrine, and aeolian factors.

The time and mode of origin is of considerable importance in any study of their subsequent history. If they were formed by a meteorite shower they are identical in age. If, then, the Pamlico terrace can be correlated with either the Peorian interglacial or the mid-Wisconsin as Cooke (1930, 1935) suggests, then the bays were formed in late Pleistocene time since only those on the Pamlico terrace are interfered with by beach ridges. Since their formation some of them have doubtless been obliterated through erosion. Some have been modified through drainage and are more or less completely under cultivation. A few contain lakes. The majority, however, are completely filled with peat.

A study of the historical record of the peat deposits will doubtless cast considerable light upon post glacial history in this area. Preliminary studies in Bladen County, North Carolina, give no indication that the bays this far inland had a marine origin or have since been invaded by the ocean as have those peat areas on the Pamlico terrace (Dachnowski-Stokes and Wells, 1929; Cocke, 1934). Pollen is abundant in most of the horizons. When a study of the pollen spectrum is completed its correlation with results of similar studies in northern bogs will prove to be of considerable value. The present paper, however, deals only with the method of peat formation as it is illustrated in the few lakes still in existence in these depressions.

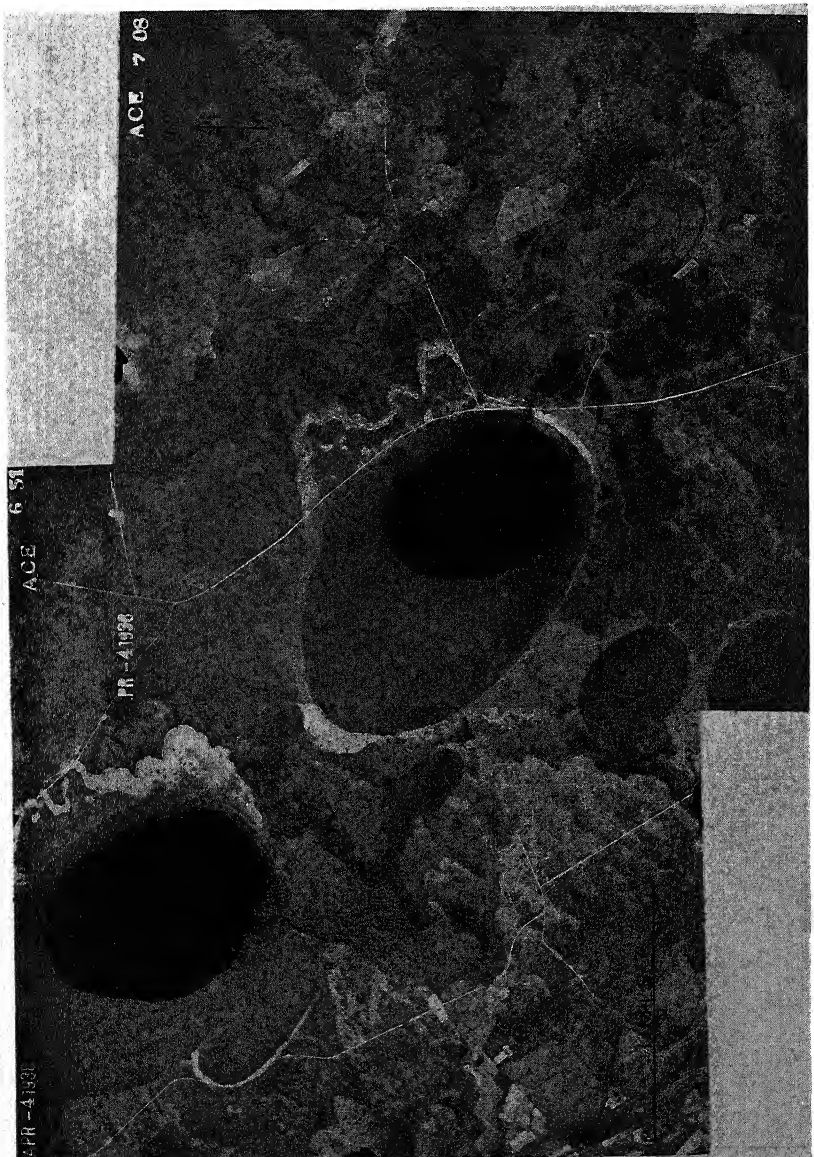

Fig. 1. Aerial photographs of a portion of Bladen County, N. C., showing Salter Lake, upper left, and Jones Lake, center. The dunes associated with these lakes lie on the east side of their basins. Several smaller "bays" filled with peat are shown. Southeast of Jones Lake are some "bays" which have been drained and are under cultivation. (*Photo by Agricultural Adjustment Administration.*)

During the course of the study of Jerome Bay, a peat deposit in Bladen County, North Carolina, it became evident that this is a filled-in lake basin. The pattern of vegetation suggested that the lake had filled in most rapidly from the north and the west sides, very slowly from the south and the east sides. Recent aerial photographs of this part of the State, which have been supplied by the Agricultural Adjustment Administration, furnish evidence that this has probably been the case. Of the several lakes which still exist in such depressions all occupy the southeast portions of their original basins. The north and west portions of the lake basins have been more or less filled in with peat.

Two features are responsible for this pattern of peat deposition. One is the direction of the prevailing winds. The second is the shape of the basins, the bottom profiles of which give promise of being constant for all the bays.

The prevailing southwest winds have favored peat deposition on the west, while slowing up the process on the east side of the lakes. That the prevailing winds have been from the southwest since the formation of the depressions is evidenced in the dunes, now stabilized, which were blown out from the sand rim at the southeast end before revegetation occurred. The winds, by accentuating wave action on the east side of the lake, greatly retard the rate of marginal encroachment and inhibit island formation about cypress bases and knees. On the lee side, quiet water prevails, and the undisturbed condition is reflected in the character of the vegetation which is vigorously invading the lake.

The second factor affecting the peat deposition in these lakes is the character of the lake basins themselves. The bottom profile along the long axis is known fairly accurately for Jerome Bay. A long, deep basin occupies the central and southern portions while at the north end there is a broad, gently sloping shelf. The deepest point, 11 feet, is at the center. South of this the deep basin extends 2000 feet, its profile rising gradually to a five foot depth 500 feet from the south end. There is then a rapid rise from this 5 foot depth to the sand rim at the south end. North of the center the basin continues deep for 500 feet but in the second 500 feet it rises rapidly to a 5 foot depth. Thence is a long gradual slope about 1500 feet northward across the broad shelf at the north end. Soundings in two nearby lakes, Jones and Salter Lakes, as well as in the surrounding peat indicate similar profiles.

That peat accumulation should be more rapid from the north end would be expected, considering the method by which peat is formed in

these southern lakes. The principal pioneer is the pond cypress, *Taxodium ascendens* Brong., which becomes established on the exposed lake bottom during the dry seasons when the water is low. Obviously over a broad shallow slope, such as is characteristic of the north ends of these depressions, broader expanses of bottom are exposed during drouths than where the bottom dips more steeply. Once the cypresses are established their buttressed bases and knees become nuclei for islands of shrubs and trees. The most common of the pioneer shrubs are *Pieris nitida* B. & H., *Cyrilla racemiflora* Walt. and *Clethra alnifolia* L. along with which a few trees, primarily *Persea pubescens* (Pursh) Sarg., *Acer rubrum* L. and *Chamaecyparis thyoides* (L.) BSP. become established. In addition to the island development about the cypress trees, there is a mass advance of the vegetation into the lake from the margin, the same species predominating. This marginal encroachment as well as the growth of the islands is accomplished through the stoloniferous habit of some of the shrubs together with the spreading superficial root systems of all the woody bog plants. A dense, strong mat is thus formed which grows out into the water. The growth of this mat is slow and it never extends more than a few feet beyond the completely peat-filled portion of the lake. Under the narrow, free outer portion of the shrub mat the gradient of the mucky lake bed is often very steep so that there may be as much as three feet of water below its edge at normal water level. A very large amount of filling in of the lake is by the wash of fine materials toward the center from this overhanging marginal mat as well as from the islands. Frequent outward drift of logs and fallen trees and their subsequent sinking to the oozy bottom adds considerably to the accumulation. Mat development dependent upon the completion of this filling in is naturally more rapid over shallower portions of the lake.

In contrast with the conditions prevailing in most northern bog lakes, in these lakes there is almost no herbaceous aquatic vegetation. In this climate pronounced fluctuation of lakes together with hard sandy bottoms may be the factors inhibiting the growth of marsh plants. Or it may possibly be the excessive staining of the water as suggested by Martin and Uhler (1939). Furthermore herbaceous plants, rather than being of primary importance in mat formation, are very scarce among the shrubs and trees that form the bog mat. The most prominent difference of all is the pioneer rôle taken by aquatic trees in the advance of the

vegetation into the lakes. This is a situation extremely different from the retarded position of trees in the aquatic plant succession in the north.

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Some New Myxophyceae from Southern California

George J. Hollenberg

(with eight figures)

Algal collections in southern California during the past several years have yielded a number of Myxophyceae of considerable interest, some of which are apparently new. Several of these are described herewith.

Myxohyella seriata sp. nov. (Fig. 1)

Plants filamentous, totally endophytic; filaments simple or sometimes dichotomously branched below, 100–140–(170)μ long; young plants and deeper portions of older plants composed of a single row of cells 3–6μ diam. and 15–30–(40)μ long; distal portion of filaments gradually larger, up to 12μ diam., the cells dividing in three planes to form a number of tiers of 4–8–(16) small cells (endospores) 2–3μ diam.; protoplasm finely and uniformly granular, very pale blue-green; sheath thin and hyaline; filaments abundant, penetrating deeply between the filaments of a species of *Isactis*.

Plantae totae endophyticae; filamentis simplicibus aut nonnullis dichotomo furcatis, 100–140–(170)μ longis; partibus profundibus ex una serie cellularum 3–6μ latis et 15–30–(40)μ longis constitutis; partibus superioribus gradatim majoribus, vel 12μ latis; nonnullam seriem stratorum ex 4–8–(16) cellulis (endosporis) parvis 2–3μ latis compositorum formantibus; protoplasma subtiliter granulosum, pallide aerugineum; vaginis tenuibus hyalinis. Hab. In *Isactis* sp.

This plant was first collected in the fall of 1934 from above high tide level at San Pedro in Los Angeles County. Later it was found abundant on spray covered rocks above high tide level near Corona del Mar in Orange County. At both of these stations it has been collected a number of times at different seasons of the year. More recently it has been collected near high tide level on the bay side of Punta Banda, Lower California, Mexico. It appears to be perennial and seems to be a common endophyte in a species of *Isactis* to which it appears to be limited. A number of specimens of *Isactis* from the Pacific Coast in the herbarium of the University of California appear to be identical with the host of *Myxohyella seriata.* Most of them were collected from the central and northern part of the state. The endophyte was not found in any of them. It seems likely, therefore, that it is a plant of warmer coasts.

Soon after the filaments become established in the host, the cells at the outer end gradually increase in size, beginning at the outermost cell. Spore formation is initiated by a longitudinal division of the outermost

cells. This division may be preceded by a transverse division. A second longitudinal division generally occurs at right angles to the first and is followed by a tranverse division. There is usually another division in an irregularly oriented plane. As a result 16–32 small cells are usually formed by division of a single cell of the filament. These apparently represent endospores which are liberated by disintegration of the parent cell wall as new ones are continuously formed by transformation of successive cells of the filament.

This plant seems amply distinct from all other species of *Myxohyella*. The very elongate cells of the deeper portions and the more or less regular divisions of the upper cells into tiers of 8–16 cells seem most distinctive features. The plant is also considerably larger than previously described members of the genus. Of the several collections made by the writer number 2379B is considered the type. It was collected from the top of a small municipal concrete breakwater at Cabrillo Beach, San Pedro, in Los Angeles County, October 22, 1938.

Entophysalis marginalis sp. nov. (figs. 3–5)

Colonies irregularly lobed, 1–3 mm. diam., firm, cartilaginous and light yellow in color; inner cells of the colony spherical or slightly oval, 2.5–3.5μ diam., mostly in pairs with a hyaline sheath, widely separated in a firm hyaline matrix, and more or less arranged in rows which radiate toward the surface of the colony; outermost cells 7–8.5μ diam.; protoplasm finely granular, pale blue-green.

Coloniae irregulariter lobatae, 1–3 mm. crassae, firmae et cartilaginosae; color diluto-flavae; cellulis interioribus globosis aut leviter ovatis, 2.5–3.5μ diam., plerumque in paribus cum vaginis hyalinis, in matrice hyalina gelatinoso-firma late separatis, plus aut minus in ordinibus dispositis, qui ad superficiem radiant; cellulis majoribus et ordinibus plus explicatis ad superficiem coloniae; cellulis extimis 7–8.5μ diam.; protoplasma tenui-granulosum, pallide aeruginosum. Hab. ad saxa praehensae.

The type material, number 1562A, was collected by the writer in October of 1936 on the leeward side of a small concrete municipal breakwater at Cabrillo Beach, San Pedro, Los Angeles County. Numerous colonies were present, covering an area a foot or more across. Sheaths around cell groups are more distinct at the surface of the colony. As a result the surface view of the colony resembles a *Gloeocapsa* (fig. 5). The sheaths and matrix near the surface of the colony are yellowish in color. Larger granules are occasionally present in the finely granular protoplasm. The close crowding and compressed shape of the superficial

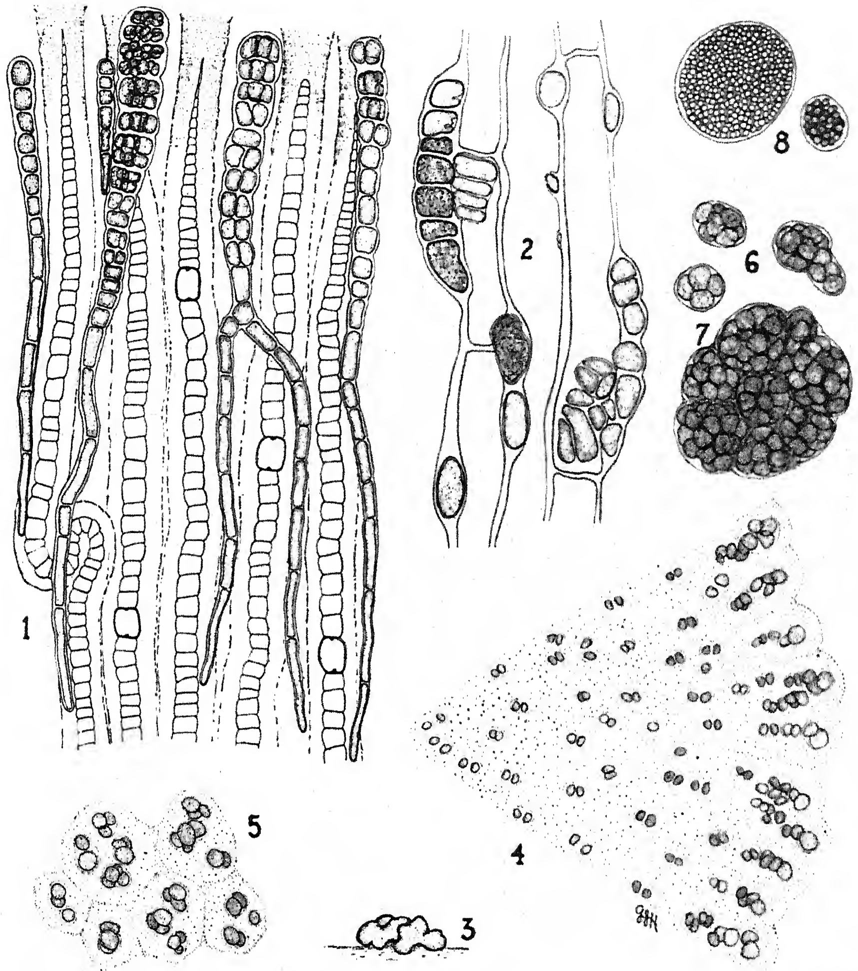

Fig. 1. Several plants of *Myxohyella seriata* sp. nov. among the filaments of the host, showing endospores forming at the outer end. ×700.

Fig. 2. *Xenococcus pulcher* sp. nov. in the walls of a species of *Chaetomorpha*, showing young stages becoming embedded in the wall of the host, mature plants, and endosporangia with endospores. ×325.

Fig. 3. Habit sketch of *Entophysalis marginalis* sp. nov. ×2.5.

Fig. 4. Thallus structure of *Entophysalis marginalis* in radial view. ×325.

Fig. 5. Surface view of a portion of a colony of *Entophysalis marginalis*. ×325.

Fig. 6. Young colonies of *Microcystis splendens* sp. nov. ×700.

Fig. 7. Older colony of *Microcystis splendens*, showing the formation of subcolonies. ×700.

Fig. 8. Colonies of *Microcystis ovalis* sp. nov. ×700.

cells suggests that they are more actively dividing than the more widely separated inner cells. The progressive decrease in size of the cells from

the surface toward the center of the colony also indicates that cell division is largely limited to the outer cells of the colony. In fact the outermost cell of each radiating row appears to function as a kind of apical cell, primarily responsible for the increase in the diameter of the colony. Frequent more or less anticlinal divisions of these outermost cells result in the gloeocapsoid superficial aspect. Cell division was the only type of reproduction observed.

The genus *Entophysalis* was for some time considered only imperfectly distinguished from *Gloeocapsa.* Gardner (1927) in discussing the genus emphasizes the importance of the fact that cell division is largely limited to one plane in *Entophysalis.* The plant here described is further distinguished by the fact that cell division is largely limited to the cells at or near the surface of the colony. *Entophysalis marginalis* is closely related to *E. granulosa* Kuetzing, the type species. A bit of the type material of *E. granulosa* has been sent to the herbarium of the University of California from the Kuetzing herbarium. A fragment of this material was examined by the writer. In *E. granulosa* the cells of the colony are nearly of the same size throughout the colony and cell division does not appear to be at all limited to the superficial cells of the colony as in *E. marginalis.* The inner cells are not so widely separated in *E. granulosa* nor are they as distinctly in pairs but the inner cells are more distinctly in rows than in *E. marginalis.*

Gardner (1927) expressed doubt concerning the presence of *Entophysalis* in this country, although an undetermined species, number 99786 in the herbarium of the University of California, was collected from rocks at high tide level at Carmel Bay in central California, presumably by either Setchell or Gardner. The latter plant resembles the southern California plant somewhat but seems nearer to *E. granulosa* in most respects, especially in the nearly uniform diameter and distribution of the cells.

Xenococcus pulcher sp. nov. (fig. 2)

Plants endophytic, solitary or aggregated, up to 25μ diam., more or less flattened, dividing in two planes only; protoplasm finely granular, distinctly reddish; endosporangia 15–20–(30)μ broad, forming numerous endospores 2–2.5μ diam. and likewise reddish in color.

Plantae endophyticae, solitariae aut aggregatae, vel 25μ latae, plus aut minus compressae, in duobus planis solum dividentes; protoplasma subtiliter granulosa sensim rubra; endosporangiis 15–20–(30)μ latis, endosporas numerosas 2–2.5μ latas formantibus. Hab. In muris *Chaetomorphae* sp.

This striking plant was found as an abundant endophyte in the walls of a minute plant which is probably an undescribed species of *Chaetomorpha*. The latter was attached to piling near low tide level on the bay side of the government breakwater at Cabrillo Beach, San Pedro, California. In habit it resembles *X. endophytica* described by Setchell and Gardner (1937) from the Galapagos Islands. It occurs in a different host but the host is often more or less distorted by the growth of the endophyte as in the case of *X. endophytica*. The plant here described differs from *X. endophytica* in the distinctly larger size of the cells and in the pronounced reddish color of all cells. The cells are mostly lenticular-compressed. They appear to possess a thin wall of their own, hardly distinguishable from the wall of the host in which they are imbedded. The plant was first collected in October of 1936. Number 2145 in the herbarium of the writer was collected a year later at the same place. It is considered the type material.

Microcystis splendens sp. nov. (figs. 6, 7)

Colonies spherical to irregular, commonly 20–50μ diam. but frequently up to 100 or even 170μ, the larger colonies often composed of subcolonies; colonial tegument thin and hyaline; cells closely packed, spherical or angular by mutual compression, 3.5–5μ diam.; protoplast brilliant blue-green, uniformly granular and without pseudovacuoles.

Coloniae sphericae aut irregulares, plurimum 20–50μ, sed saepe 100 aut 170μ crassae; coloniae majores saepe ex subcolonis constitutis; tegumentis colonarum tenuibus et hyalinis; cellulis globosis aut plerumque per pressuram angulatis, 3.5–5μ crassis; protoplasma tenui-granulosum, splendido-aeruginosum.

The brilliant blue-green color seems distinctive. Colonies break up and start new colonies, separating readily with a slight pressure on the cover glass. Application of a solution of methylene blue shows the absence of a sheath around the individual cells when so separated, although narrow colorless sheaths are quite evident around even very small colonies. This interesting plant has appeared several times in old culture dishes of germlings of brown algae in the laboratory at La Verne College, frequently in company with *M. ovalis* of this paper. In the cultures the colonies were attached to the glass slides and eventually became very abundant in the culture dishes. Type material Hollenberg number 2179C.

Microcystis ovalis sp. nov. (fig. 8)

Colonies simple, spherical or commonly oval and smooth in outline, with distinct hyaline tegument; cells closely packed, spherical, 1.5–2μ diam.; pro-

toplast pale blue-green or slighly olivaceous, without pseudovacuoles or conspicuous granules.

Coloniae simplices, globosae aut plerumque ovatae et leves, cum tegumentis distinctis et hyalinis; cellulis globosis 1.5–2μ crassis, confertim compressis; protoplasma pallidum et plus aut minus luteolum aeruginosum, sine granulis conspicuis.

Microcystis ovalis has been encountered several times in old cultures of germlings of marine algae kept in the laboratory at La Verne College, La Verne, Cailfornia. The plants multiplied rapidly in the culture dishes throughout the summer and fall of 1938. The cells appear to be smaller than those of previously described marine members of the genus. Type material, Hollenberg number 2179D.

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INDEX TO AMERICAN BOTANICAL LITERATURE

The aim of this Index is to include all current botanical literature written by Americans, published in America, or based upon American material; the word America being used in the broadest sense.

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Controlled Differentiation in a Plant Tissue Culture

PHILIP R. WHITE

(WITH TWO FIGURES)

The attempt to grow isolated organs, tissues, or cells of animals or plants has as one of its objects the study of the cell in relation to its environment, including other cells and tissues of the organism. In providing an artificial environment capable of supporting normal survival and growth of the isolated tissue or organ, we are replacing the effects of the contiguous tissues by known and controllable factors. The question of whether or not the cultivated cells possess all the capacities of the entire organism does not necessarily arise. The cell need not be looked upon as totipotent.

If we are dealing not with single cells but with cell groups, as in fibroblast cultures or callus cultures, and if we are to assume that the metabolism of the individual cell is correctly represented in that of the mass, it is indeed essential that the culture shall not differentiate. While all somatic cells may in theory be looked upon as being totipotent elementary organisms, this totipotency must remain unexpressed if cultures of this kind are to be suitable for such studies. The importance of an undifferentiated body of cells in tissue culture work is thus evident and has received much emphasis in discussion to date. But, while it is important to be able to maintain cultures in an undifferentiated state in order that results may be interpreted, it is also highly desirable, at least from a theoretical point of view, to *know* how broad or how restricted are the real capacities of the cells in question, if they are totipotent or are restricted in their capacities. And, if their capacities are restricted, what is the degree and nature of this restriction?

The studies of animal organization carried on so extensively by the followers of Spemann lend considerable support to the point of view that the cell is totipotent, that its differentiation is, in the main, directed from

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outside the cell although the details of that differentiation are inherent in the organism. Studies of teratomas in general support the same concept. Animal fibroblast cultures, on the other hand, maintain their individualities for many generations and show only a restricted capacity of transformation to other cell types, to monocytes but not to epithelium, for example. These pure-line fibroblast cultures have for a long time represented one of the most serious stumbling blocks to acceptance of the concept of the cell as a "totipotent elementary organism." The root cultures carried on for the past decade in this laboratory and elsewhere have likewise failed to give evidence supporting the "totipotent" concept of the cell. Tomato roots have shown no sign of differentiating stem or leaf tissues nor of dedifferentiating to form simple parenchyma. They have always remained roots. They appear to be endowed with only a part of the capacities of the intact tomato plant, although they do form a considerable number of different cell types having different physiological functions. The callus cultures from the hybrid *Nicotiana glauca* × *N. langsdorffii*, maintained in this laboratory for the past year and a half and recently described (14), not only do not form organs but have actually formed only two types of mature cell—the very simple pith cell and the scalariform cell. These cultures might seem, therefore, to support the idea, which has become rather widely accepted in the last few decades, that there exists a definite and irreversible segregation of capacities among different regions and cells of any given organism.

It is the purpose of this paper to present evidence that this obvious interpretation of the behavior of these callus cultures is, in fact, fallacious and to show one way at least in which the totipotency of the tissues can be demonstrated.

EXPERIMENTAL

Excised tomato roots ordinarily float at or near the top of the nutrient so that a large part of their surfaces lies not more than a millimeter or two from the air. Their supply of oxygen may be assumed to be quite adequate. When, as occasionally happens, roots do not float but sink to the bottom of the nutrient, they generally grow poorly, but it is not possible to say if this is the result of their sinking or if their submergence is itself evidence of low vitality. Whatever may be the primary limiting factor in this chain of events, the idea has grown up that, in order to obtain the best results with such cultures, it is desirable to give them a maximum contact with the air compatible with maintaining a satisfactory nutrient supply to the tissues. In cultivating callus masses of various

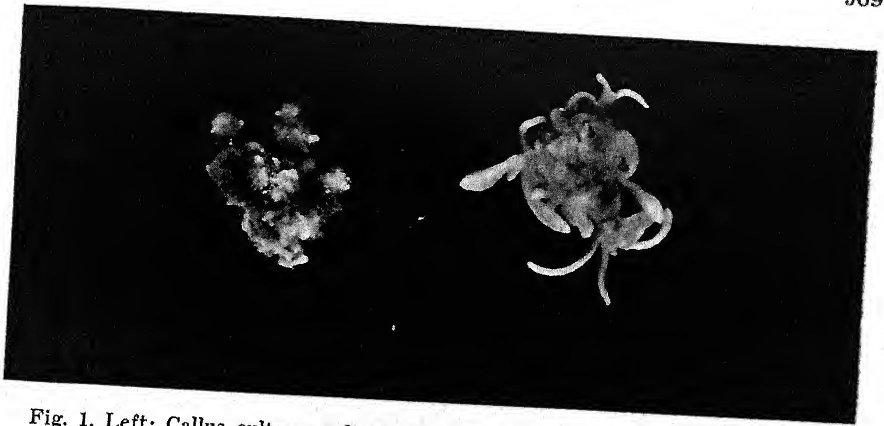

Fig. 1. Left: Callus culture undivided for 20 weeks, grown on a semi-solid culture medium. Right: A similar culture grown for 10 weeks on a medium like that at the left, then transferred for 10 weeks to a liquid medium containing the same nutrient materials. ×2.

Fig. 2. A callus culture maintained for 8 weeks in an undifferentiated state by repeated transfer on a semi-solid nutrient and then placed for 2 weeks on a liquid nutrient. ×8.4.

kinds, Gautheret (2, 3) and Nobécourt (6) both found that growth occurred only in the portions of cultures which projected above the surfaces of the semi-solid substrata employed in their experiments. In attempting to cultivate callus in this laboratory, the solution developed for excised roots was first tested. Tissue fragments suitable for such cultures regularly sank to the bottom of the solution. To remedy this, a semi-solid nutrient capable of supporting the cultures was provided by adding 0.5 per cent of thoroughly washed agar to the above solution. Under these conditions a continuous, healthy-appearing callus growth was obtained without evidence of differentiation even after 20 or more weeks on such a substratum.

A few cultures, however, were reintroduced into the unmodified liquid medium with interesting results. Callus which had been maintained in an undifferentiated state by cultivation on a semi-solid medium for 10, 25, and 40 passages was allowed to stand in the liquid nutrient without being subdivided. After periods varying from 2 to 8 weeks, such cultures regularly underwent a marked transformation. Stem growing-points were differentiated at or near the surface of the cell masses. These developed into short stems, and typical small leaves were formed in exactly the manner so characteristic of these calluses when attached to the plant (figs. 1 and 2). It is well known that innumerable tiny leafy shoots regularly form on the callus overgrowths formed *in situ* (5). The shoots formed on excised callus when grown in liquid nutrient were entirely similar, with well formed green leaves and quite normal appearance.

Efforts to root leafy cuttings taken either from excised callus grown *in vitro* or from *in situ* callus have both so far failed. It is, therefore, not certain that these shoots possess all of the potentialities of the entire plant. It is, however, clear that they do possess a great many of these potentialities, far more than were evident in the undifferentiated callus cultures. In addition to the two types of cells formed on agar nutrients, these masses give rise, in a liquid nutrient, to mesophyll and palisade cells, epidermis bearing stomata and well formed glandular hairs, vascular strands, etc. They have not yet produced roots. This change in behavior has been brought about by the simple expedient of immersing the tissue mass under about 8 mm. of liquid instead of exposing it on the surface of the medium.

DISCUSSION

What factor in this treatment is responsible for this change in behavior? The experiments carried out to date do not permit a definite

answer. The most obvious difference introduced is, as has been suggested, a difference of oxygen supply. When cultures are grown on nutrient agar, the air is in contact with a large part of their external surfaces and, through the open lacunae so evident in section (14, fig. 5), with a considerable proportion of the cells of the interior. Since photosynthesis presumably does not go on in these cultures, the gaseous exchange is merely that of absorbing oxygen and releasing CO_2. The characteristics of the culture and its surroundings permit this exchange to go on freely. Only in the interior of the cultures is there likely to be a deficiency of available oxygen, and it is precisely in the interior that the only differentiated cells, the scalariform cells, occur.

In cultures grown under a layer of liquid nutrient, these conditions of free gaseous exchange do not exist. Oxygen is but slightly soluble in water and in aqueous nutrients, and a sharp oxygen gradient exists between the liquid-air interface and the subsurface regions (15). The tissue, lying under about an 8 mm. layer of nutrient, is cut off from direct contact with the air and placed under conditions likely to result in an oxygen deficiency not only in the interior of the cell masses but at their surfaces as well. Bouillenne and Prevot (1) and Prevot (7, 8) have shown that anaerobic conditions favor the production of buds in *Begonia* and other plants. Priestley and his coworkers (9, 10) believe that pH gradients may be causally involved in the direction of meristematic activity. Lund and his school (11, 12) find that electropotential gradients are regularly associated with and greatly affected by conditions modifying the behavior of meristems. Both acidity and electropotential are, of course, largely influenced by respiration processes. There thus seems to be considerable evidence already in the literature to suggest that reduced oxygen supply may serve to orient the development of a tissue. The results of these experiments with excised plant callus fit satisfactorily into this hypothesis, although the evidence is as yet too meagre to permit a definite explanation.

Whatever the true explanation of this phenomenon may be, it is important to note that here we have taken groups of cells which for 10, 25, and 40 passages had appeared to have lost most of their capacity to differentiate, and by a very simple experiment have shown this appearance to have been false, to have been due merely to the conditions of the experiment. These cell groups are nearly, if not completely, "totipotent." They represent in a very real sense, "elementary organisms." We begin to get a glimpse into the mechanisms that control development. And these mechanisms, in this case at least, involve no complicated "hormone" con-

cept. We have produced caulices without "caulines," phyllices without "phyllocalines," just as in earlier work with roots we produced radices without evident "rhizocalines." Oxygen gradients, as long ago indicated implicitly by Rosene and Lund (11, 12) and others and as suggested by some of Thimann and Sweeney's recent work on cyclosis (13), may actually be responsible for many complex correlation phenomena.

SUMMARY

Cultures of callus from a hybrid *Nicotiana* which, on a semi-solid nutrient, have been maintained in an undifferentiated state through many passages can be made to form leafy branches of a high degree of differentiation by immersing them in a liquid nutrient. It is suggested that oxygen gradients may be important factors in controlling differentiation. Some of the implications of this observation for the concept of the cell as a totipotent elementary organism are briefly mentioned.

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The Genus Stereum in Pennsylvania[1]

L. O. Overholts

(with plates 14 to 18)

Among the wood-inhabiting fungi of Pennsylvania no species are more frequently encountered than the sessile members of the Family Thelephoraceae. Nor are the members of any genus more easily recognized on sight than are the members of the genus *Stereum*. Except for the species of Hymenochaete, almost any sessile or effused-reflexed fungus with smooth hymenium (i.e., no teeth, warts, gills, or pores) is safely referable to *Stereum*. Unfortunately, most of the wood-inhabiting species of the genus have the habit of growing in resupinate condition if the substratal surface is not conducive to pileus formation. The situation is similar to the relation one finds between the genus *Poria* and the genus *Polyporus* of the Polyporaceae. Fortunately, however, in most cases resupinate specimens of species of *Stereum* can be distinguished from such similar genera as *Corticium* and *Peniophora* by the presence of a cuticular layer (figs. 15, A and 16, A) of dense hyphae lying between the main body of the context and the substratum and connected to the latter by a loose tomentose layer. These two layers, tomentose and cuticular, are actually the representatives of the superficial pubescence and the layer from which it arises in the pileate condition.

A few species of *Stereum* are terrestrial and centrally or laterally stipitate (figs. 13, 14). Such are to be distinguished from *Thelephora* by the nearly or quite colorless tissue of the sporophore and the hyaline and smooth spores.

The hymenial structure of species of *Stereum* shows no outstanding characteristics not found in other genera of Higher Basidiomycetes. Cystidia or gloeocystidia are present in some species and when present show the usual variations found in similar groups. Vesicular cells (fig. 17) are present in a few species and paraphyses of diagnostic value are sometimes present. Structures of this sort can be demonstrated in crushed mounts of the tissue of the sporophores but are best seen in vertical sections, cut free hand, through the sporophore. In cutting such sections it is advisable to so orient the cuts that they are made parallel with the hyphal tissue of the pileus, i.e., in a radial direction. KOH is best used as a mounting fluid and the sections may be stained with phloxine or eosin.

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In general spores are not easily obtained except from sections. Their small size and the fact that they are colorless renders their detection difficult unless present in abundance.

Burt lists about 80 species of the genus in North America. This includes a considerable number of tropical and subtropical species. A number of others are known only from limited ranges in various parts of the country. We have recognized 27 species occurring in Pennsylvania. Undoubtedly a few others will yet be found. The state has not been covered in any systematic fashion but collecting has been done in a considerable proportion of the counties. Fortunately, they are fungi that persist throughout the year and can be collected in at least fair condition winter and summer, although reaching the height of their development in late summer and autumn.

Economically the importance of the species lies in their wood-destroying propensities. They are among the most important wood-scavengers of the forest, attacking especially the sapwood of slash and stumps. Three or four species are of importance as heart-rotting organisms in living trees and in old logs. *Stereum gausapatum* has recently been shown to be of great importance as a heart-rot of sprout oak growth, and *S. sanguinolentum* is coming into prominence as a decay organism in living conifers. *S. frustulosum* produces a pocket type of heart-rot in chestnut and oak and *S. subpileatum* is of importance in a number of other hardwoods. All of the wood-inhabiting species are easily obtained in culture.

GENERIC DESCRIPTION

Sporophore terrestrial or epixylous, stipitate, sessile, effused-reflexed, or largely resupinate, tough to leathery and somewhat woody; context white or somewhat colored but not darkening in KOH, usually bordered above by a definite narrow zone of compacted hyphae (cuticular layer) bearing the tomentum; hymenium inferior, even or nearly so; cystidia, gloeocystidia, vesicular cells, and prominent paraphyses sometimes present; setae none; spores hyaline or in a few cases tinted with age.

KEY TO THE SPECIES IN PENNSYLVANIA

1. Sporophore stipitate, the stem central to lateral but not horizontal nor in the same plane with the pileus; growing on the ground........................ 2

   Sporophore sessile, effused-reflexed, or resupinate, rarely with a stem-like base in the same horizontal plane as the pileus; growing on wood................ 3

2. Pileus 1–2 cm. broad, brown or hazel on drying; stem 2–4 mm. thick; pileus 200–300μ thick; spores ellipsoid or oblong, 4–5$\times$2–2.5μ; cystidia numerous... ....*S. diaphanum*

   Pileus less than 1 cm. broad, drying pallid; stem about 1 mm. thick; pileus 400–800μ thick; spores subglobose, 4–4.5μ diameter; cystidia none......*S. Burtianum*

3. Sporophore small, convex or tuberculate, thick, cushion-shaped, not pileate, rarely as much as 0.5 cm. broad 4

Sporophore sessile or effused-reflexed or if resupinate then either more than 0.5 cm. broad or else not convex nor tuberculate 5

4. Sporophore red or reddish, waxy when fresh; on *Populus* only .... *S. rufum*

Sporophore white or yellowish, hard and rigid when fresh; on *Quercus* and *Castanea* only .... *S. frustulosum*

5. Context containing vesicular bodies, best seen in thin sections but usually discernible in crushed mounts 6

Context not containing vesicular bodies 8

6. Sporophore corky when fresh, hard when dry, rather thick, not bending without breaking .... *S. Murrayi*

Sporophore coriaceous when fresh or when revived, often drying rigid but not hard 7

7. With slender unincrusted cystidia 4–5μ diameter projecting from between the basidia .... *S. rugosiusculum*

With subconical incrusted imbedded cystidia .... *S. Pini*

Without cystidia .... *S. purpureum*

8. Growing on wood of coniferous trees 9

Growing on wood of deciduous trees 17

9. Cystidia absent 10

Cystidia present, not heavily incrusted 12

Cystidia present, heavily incrusted in KOH 16

10. Hymenium and context deep brown in color .... *S. radiatum*

Hymenium and context pallid to gray or smoky 11

11. Hymenial region soon layered by perennation .... *S. rugosum*

Hymenial region not layered .... *S. sanguinolentum*

12. Context (or subiculum) hyphae hyaline and more or less gelatinized; gloeocystidia present; cystidia colorless; growing only on small branches of *Pinus Strobus* .... *S. Pini*

Context hyphae at least partly colored throughout; growing on logs and stumps of conifers; cystidia at least partly colored 13

13. Cystidia scarcely or not at all projecting, short-cylindric or conic .... *S. Chailletii*

Cystidia long-cylindric, protruding 50μ or more, though easily broken off at the surface of the hymenium 14

14. Tissue becoming black in KOH, unchanged in H_2O or lactic acid .... *S. ambiguum*

Tissues not darkening in KOH 15

15. Sporophore anise-scented when fresh, effused-reflexed .... *S. rugisporum*

Sporophore not anise-scented, usually entirely resupinate .... *S. abietinum*

16. Cystidia 8–12μ diameter, colorless .... *S. sulcatum*

Cystidia 6–8μ diameter, brown .... *S. Chailletii*

17. Incrusted cystidia present in the hymenium 18

Cystidia if present not heavily incrusted 23

18. Cystidia up to 10μ diameter 19

Cystidia reaching diameters of more than 10μ 20

19. Context and hyphae brown; no conspicuous paraphyses in the hymenium........ *S. umbrinum*

Context and hyphae pallid or colorless; with aculeate paraphyses in the hymenium .... *S. subpileatum*

20. Hymenium brown in mature specimens........ 21

Hymenium white, gray, smoky, or drab........ 22

21. Cystidia only up to 12μ diameter; spores $8–11\times3–4.5\mu$........ *S. albobadium*

Cystidia up to $16–20\mu$ or more diameter; spores $5–7\times2–3\mu$........ *S. versiforme*

22. Sporophore less than 400μ thick (exclusive of tomentum); spores narrow-cylindric, $5–7\times1.5–2\mu$; all cystidia projecting only slightly, $40–50\times15–20\mu$........ *S. erumpens*

Sporophore more than 400μ thick; spores $10–12\times6\mu$; some cystidia projecting $40–70\mu$, $50–120\times12–20\mu$........ *S. cinerascens*

23. Narrow filiform paraphyses with antlered branching present in the hymenium; no cuticular layer present; young hymenium more or less lavender........ *S. roseocarneum*

Without paraphyses; cuticular layer usually present........ 24

24. Conspicuous gloeocystidia present in the hymenium........ *S. fuscum*

Without gloeocystidia though narrow colored conducting hyphae may be present. 25

25. Cuticular layer lacking when vertical sections are examined........ 26

With a definite cuticular layer, usually appearing as a dense golden zone under the tomentum........ 27

26. Pileus strongly hirsute or tomentose; with inconspicuous cystidia that barely project above the level of the hymenium; on various hardwoods, seldom on *Carpinus* .... *S. ochraceoflavum*

Pileus radiately silky-fibrillose; practically confined to *Carpinus*........ *S. sericeum*

27. Colored conducting hyphae numerous when thin unstained sections of the hymenium are observed; hymenium discoloring readily to dark red when wounded in fresh specimens 28

Colored conducting organs few or none; the fresh hymenium not discoloring reddish 29

28. Pileus tobacco-colored above, radially crisped and folded, villous to hirsute; hymenium region not zonate in sections........ *S. gausapatum*

Pileus whitish to grayish, not crisped nor folded, silky to tomentose; hymenial region becoming zonate........ *S. rugosum*

29. With very inconspicuous cystidia in the hymenium, these the same diameter as the basidia but projecting up to 15μ; pileus with a soft white villous tomentum; hymenium bright yellow in fresh specimens........ *S. ochraceoflavum*

No cystidia; pubescence and hymenium coloration different........ 30

30. Pileus uniformly strigose-hirsute or hirsute-tomentose, gray, not crisped nor folded........ *S. hirsutum*

Pileus strigose hairy at the point of attachment, more glabrous or fibrillose-striate toward the margin, typically crisped and folded, more or less hazel at maturity .... *S. rameale*

Pileus short-tomentose or villous-tomentose, not crisped nor folded........ *S. fasciatum*

SUPPLEMENTARY SYNOPSIS OF SPECIES

Stipitate species growing on the ground........ *S. diaphanum* and *S. Burtianum*
Sessile species, growing on wood

With non-incrusted cystidia only .... *S. abietinum*, *S. Chailletii*, and *S. ochraceoflavum*, the latter on hardwoods only, the two former on conifers only.
With heavily incrusted cystidia only
  On coniferous wood .... *S. sulcatum*
  On deciduous wood
    Cystidia up to 10μ diameter .... *S. umbrinum* and *S. subpileatum*
    Cystidia more than 10μ diameter .... *S. cinerascens*
With gloeocystidia only .... *S. fuscum* and *S. rufum*
With inflated thin-walled vesicular cells only .... *S. Murrayi* and *S. purpureum*
With colored conducting hyphae only
  On coniferous wood .... *S. sanguinolentum*
  On deciduous wood .... *S. rugosum* and *S. gausapatum* (occasionally *S. fasciatum*, *S. rameale*, and *S. hirsutum* would be sought here).
With paraphyses only .... *S. frustulosum* and *S. roseocarneum*
With both incrusted cystidia and branched or bottle-brush paraphyses
  Cystidia not more than 12μ diameter .... *S. albobadium* and *S. subpileatum*
  Cystidia 15–20μ diameter .... *S. versiforme*
With both vesicular cells and non-incrusted cystidia .... *S. rugosiusculum*
With both vesicular cells and heavily incrusted cystidia .... *S. Pini*
With no such sterile structures
  On coniferous wood .... *S. radiatum*
  On deciduous wood
    Without a cuticular layer .... *S. sericeum*
    With a cuticular layer
      In section 200–300μ thick (exclusive of tomentose layer) .. *S. ochraceoflavum*
      In section 300–1000μ thick
        Pileus hirsute .... *S. hirsutum*
        Pileus tomentose .... *S. fasciatum*
        Pileus radially fibrillose, strigose at base .... *S. rameale*

DESCRIPTIONS OF SPECIES

1. *Stereum abietinum* Fries

Occasionally sessile with narrow pileus less than 1 cm. long, the surface brown or blackish brown, sulcate, uneven, tomentose, more frequently entirely resupinate, the hymenium at first brown with a pale margin, grayish-cinereous or with a purplish cast at the maturity of the spores, finally uniformly brown or blackish; in section 200–2000μ thick exclusive of the tomentose layer, not darker in KOH than in lactic acid, with a black cuticular layer and a broad context layer with hyphae 2–4μ diameter, next the cuticular layer these hyphae dark brown and horizontally arranged, curving into the pale hymenial region which becomes several layered with the old layers black, the annual hymenial layers 100–180μ broad; spores ellipsoid-elongate, then cylindric, 7–15 × 3–4μ; cystidia cylindric, reaching lengths of 300μ, 6–10μ diameter, hyaline or nearly so on the projecting portion which may be as much as 60–80μ in length, brown below and in the older layers, thick-walled below, thinning out at the apex, sometimes slightly rugose but not incrusted.

On dead wood of coniferous trees. Although widely distributed in the eastern United States I have but a single Pennsylvania collection. This has the

hymenial color of *S. ambiguum* as illustrated by Litschauer (Archiv. f. Protist. 72: pl. 19, fig. 1). None of my other collections show this color which I take to represent a young stage. I take the failure of the tissue to blacken in KOH to be the best separating character between *S. abietinum* and *S. ambiguum* as pointed out by Burt. Two of the eight collections in my herbarium were identified and cited by Burt. Additional specimens are at hand from Ontario New Hampshire, Tennessee and Idaho.

2. *Stereum albobadium* (Schw.) Fries (fig. 6)

Largely or entirely resupinate, but sometimes with a narrow reflexed margin which is pubescent and brown in color, coriaceous, at first appearing in orbicular patches with hymenium even, velvety, dark brown, with a conspicuous white margin; in section 200–550μ thick, with no well developed cuticular and tomentose layers, the bulk of the context consisting of somewhat parallel and longitudinally arranged hyphae, 2–4μ diameter, brown-tinted; spores cylindric, smooth, hyaline, 7–10$\times$3–4μ; cystidia rather abundant in the basidial layer, sometimes not conspicuous, projecting only slightly, 30–50$\times$8–12μ diameter, incrusted; branched paraphyses about 1μ diameter abundant in the basidial layer, rather conspicuous in young parts of the hymenium, more obscure when in fruiting condition, brownish.

On dead wood of deciduous trees. The species seems to be rare in Pennsylvania, a single collection having been recorded. It differs from *S. versiforme* in the much smaller cystidia. Additional specimens are at hand from Tennessee, Georgia, Florida, Missouri and Idaho.

3. *Stereum Burtianum* Peck (fig. 14)

Sporophore stipitate, some specimens with circular and infundibuliform pileus, but mostly split down one side and broadly flabelliform or spathulate though never plane, occasionally multiparted, 1.5–2.5 cm. tall, the pilei less than 1 (rarely 2) cm. broad, thin and pliant, white to pale fox-colored above when fresh, drying brown or pale hazel but the margin usually remaining whitish, the surface marked with radiating fibers, the margin usually even; hymenium drying nearly pallid (said to be at first yellow), smooth; stem brown, finely velutinate, about 1 mm. thick, with a fox-colored mycelium on

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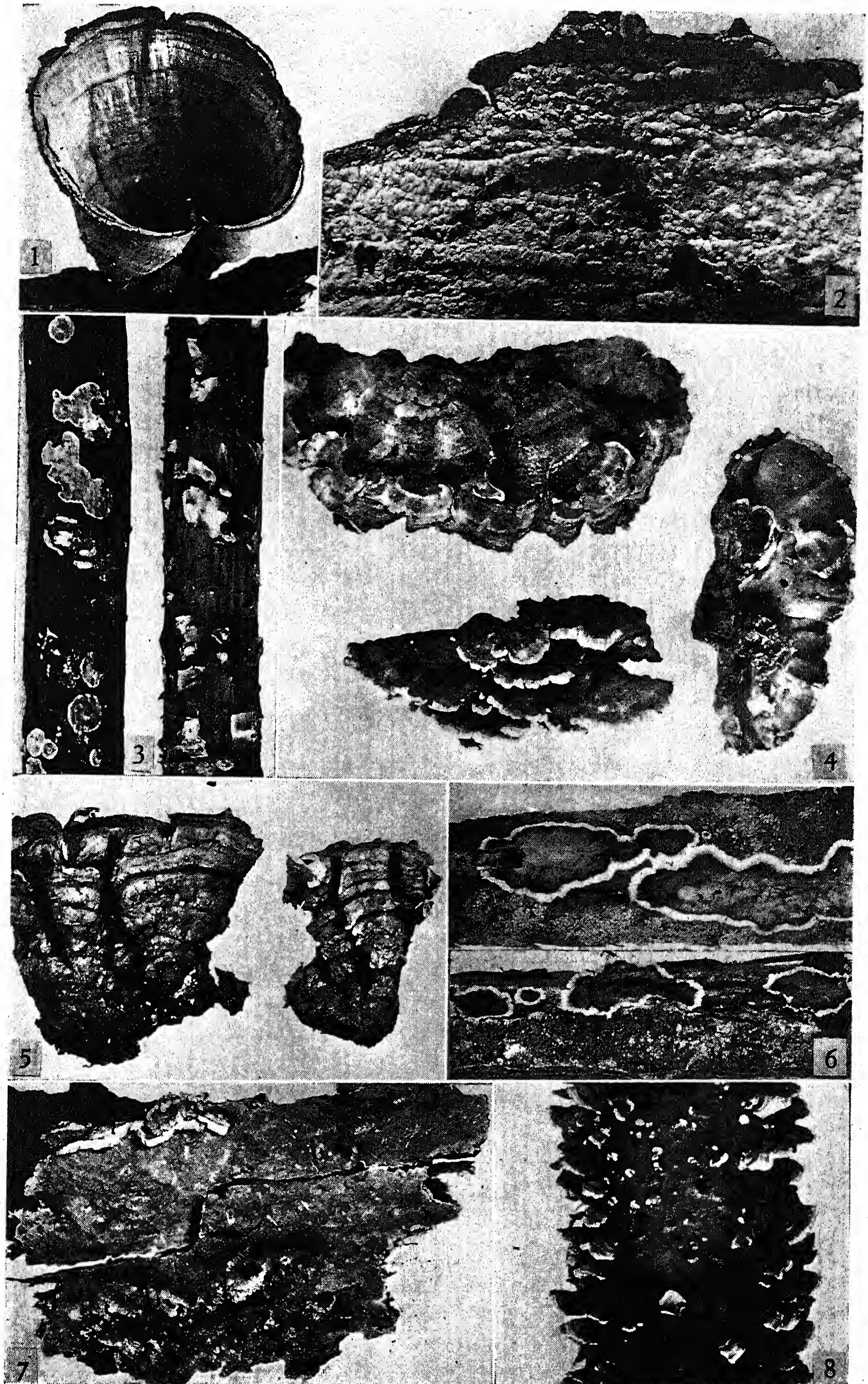
Explanation of Plate 14

Fig. 1. *Stereum fasciatum,* atypical sporophore from top of log.
Fig. 2. *S. Murrayi.*
Fig. 3. *S. Pini.*
Fig. 4. *S. gausapatum.*
Fig. 5. *S. fuscum.*
Fig. 6. *S. albobadium.*
Fig. 7. *S. umbrinum.*
Fig. 8. *S. rameale.*



OVERHOLTS: STEREUM

the ground at its base; spores globose or subglobose, smooth, hyaline, 4–4.5μ diameter or 4$\times$3μ; cystidia and gloeocystidia none; in section 400–800μ thick, of parallel hyphae 2–3 diameter, septate; cystidia none.

On sandy banks in woods. Gregarious. July to September. Except for *S. diaphanum*, which differs widely in size, this is probably the only one of the soil-inhabting species that need be expected in Pennsylvania. Additional collections are at hand from Virginia, Tennessee and North Carolinia.

4. *Stereum Chailletii* Pers.

Usually resupinate, sometimes with a slightly reflexed margin up to 5 mm. broad, or the margin merely elevated and loosened, coriaceous, pale brown, becoming blackish, narrowly sulcate, tomentose; hymenium gray to pale brown, sometimes slightly tuberculate, even or slightly cracked on drying; in section 400–800μ thick, with a cuticular layer, a tomentose layer and a broad context, the latter composed of loosely arranged hyphae 2–4.5μ diameter, hyaline to chestnut-brown; spores ellipsoid-cylindric to cylindric, smooth, hyaline, 5–8$\times$3–3.5μ; cystidia numerous in the hymenial region, brownish, rough-walled or lightly incrusted at the apex but incrustation dissolving in KOH, 5–8μ diameter, easily seen to be the termini of brown thick-walled hyphae of the context region.

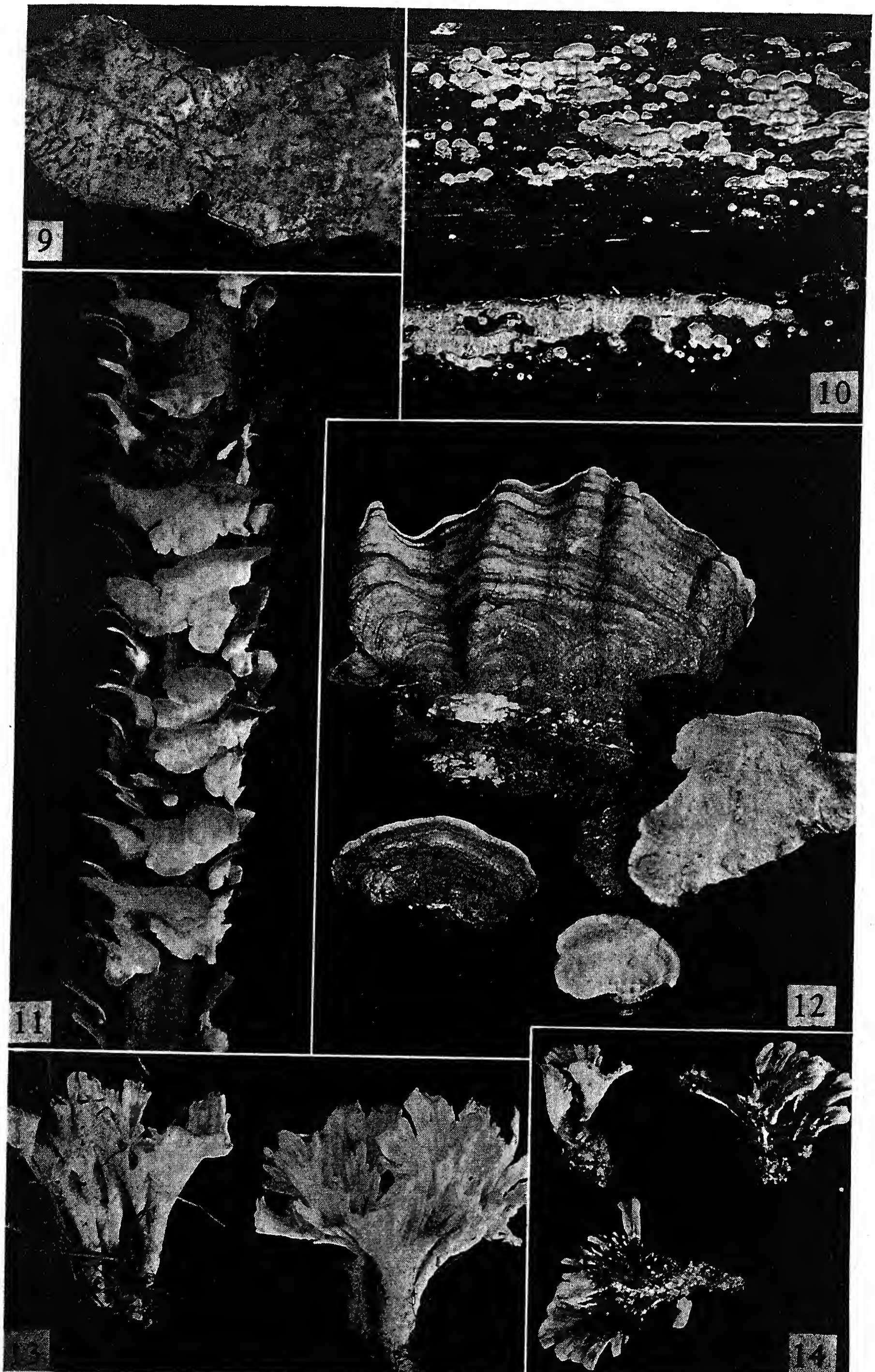
On bark of various coniferous trees. A single collection has been made in Pennsylvania. Additional specimens are at hand from Ontario and Idaho.

5. *Stereum cinerascens* (Schw.) Massee (fig. 31)

Typically effused-reflexed but often almost entirely resupinate, the pileus less than 1 cm. long, coriaceous, gray to pale tan, hirsute-tomentose; context white or pallid; hymenium slightly pubescent under a lens, gray to smoky, even; in section 300–800μ thick (exclusive of the tomentose layer), with a definite cuticular layer, the context homogeneous, composed of closely interwoven horizontal hyphae 2–4μ diameter, becoming suberect in a narrow subhymenial zone, hyaline or dilute brown; spores at first ellipsoid, subcylindric at maturity, hyaline, smooth, 9–12 (–15)$\times$5–7.5μ; cystidia usually rather abundant, conical, limited to the hymenial region, some projecting up to 60μ, others barely reaching the hymenial layer, heavily incrusted, hyaline or becoming brownish on the imbedded portion, 50–160$\times$8–20μ.

Explanation of Plate 15

Fig. 9. *S. rugosum.*
Fig. 10. *S. roseocarneum.*
Fig. 11. *S. sericeum.*
Fig. 12. *S. subpileatum.*
Fig. 13. *S. diaphanum.*
Fig. 14. *S. Burtianum.*



OVERHOLTS: STEREUM

On dead wood of deciduous trees. The species is distinct in the large incrusted cystidia and large spores. Additional specimens are at hand from Quebec, Vermont, New York, Minnesota and Nebraska.

6. *Stereum diaphanum* (Schw.) Cooke (fig. 13)

Growing singly and pileus 1–3 cm. broad or cespitose in clusters 3–5 cm. broad, stipitate, thin, tough and very flexible, entirely white or pale straw-color, depressed to infundibuliform, with margin entire or deeply split into spathulate or fan-shaped segments, fibrillose and sometimes crested on the upper surface; stem 0.5–2.5 cm. long, expanded upward, white-floccose or white-tomentose, 2–4 mm. diameter; in section 80–300μ thick, composed of closely compacted, hyaline, horizontal hyphae, 2–4μ diameter; hymenium white or light cream, more or less ridged or sometimes even in small plants; spores short-ellipsoid to oblong-ellipsoid, smooth, hyaline, 4–5$\times$2–2.5μ; cystidia numerous, some scarcely projecting, others projecting up to 60μ, 6–12μ diameter, with some crystalline material that dissolves in KOH, cylindric, blunt at apex.

On the ground in woods or on lawns under trees. This is one of but two ground-inhabiting species to be expected in Pennsylvania. It is rare, however. Additional specimens are at hand from Quebec, Ohio, Indiana and Missouri.

7. *Stereum fasciatum* Schw. (figs. 1, 29)

Sessile or effused reflexed, 2–8 cm. long, 2–6 cm. broad, less than 1 mm. thick, often laterally coalesced, thin and flexible when fresh, only partly rigid when dry, typically narrowly attached by a substipitate base but where effused-reflexed this not apparent, fan-shaped to dimidiate, rather a uniform gray in color but becoming darker and often greenish at the base, often reviving with marginal growth and then the second year's growth much lighter in color than that of the first year, more or less zonate and sometimes rather narrowly multizonate, covered by a thin compact tomentum which wears away exposing zones of hazel; context pallid to wood-color; hymenial surface gray to smoky or pale yellowish-tan, smooth and even; in section 600–1000μ thick,

Explanation of Plate 16

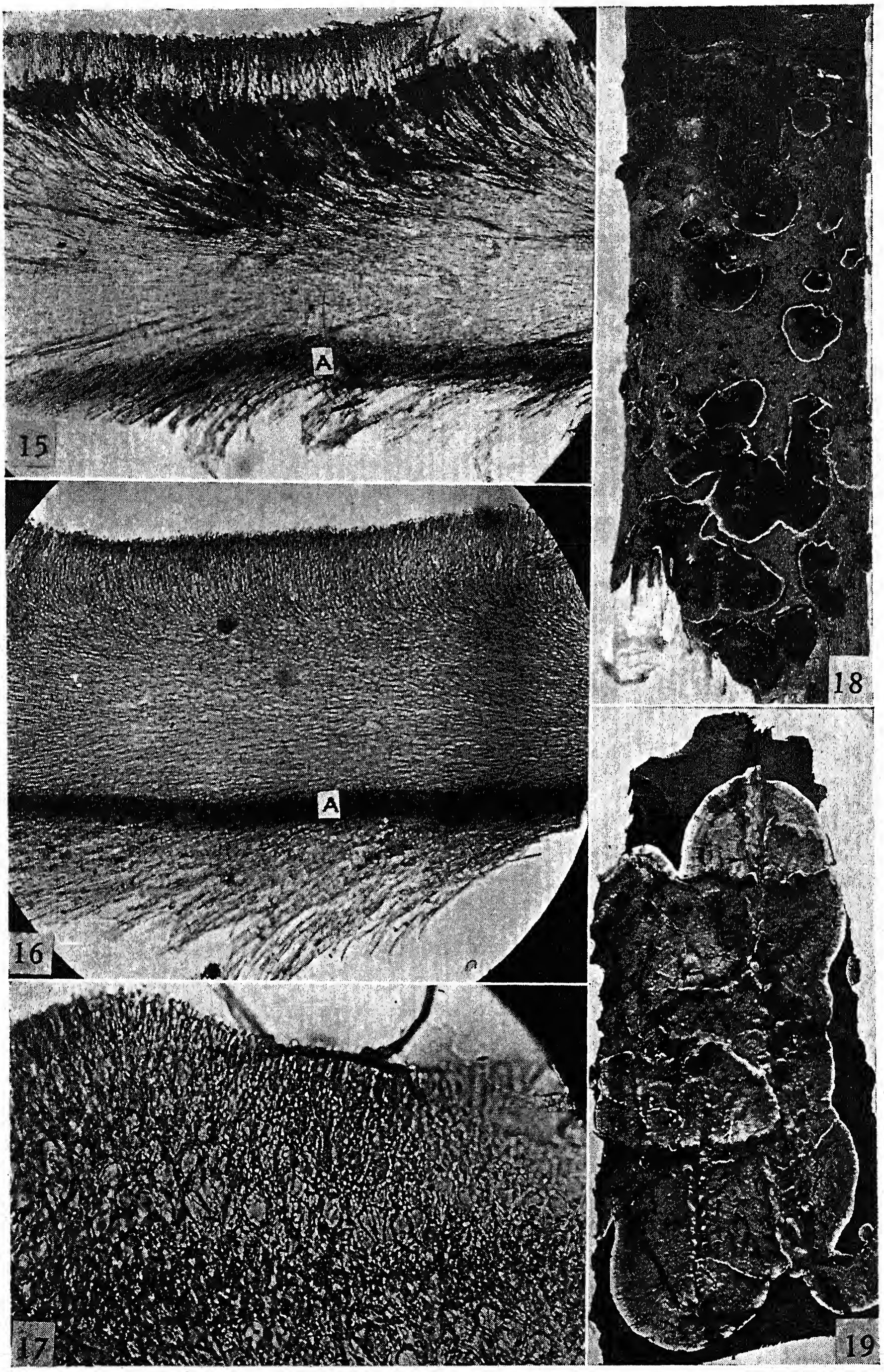
Fig. 15. *S. sanguinolentum.* Photomicrograph of vertical section through sporophore, showing the numerous dark colored conducting hyphae in the hymenial and subhymenial region and the cuticular layer under the superficial tomentum.

Fig. 16. *S. hirsutum.* Vertical section through sporophore, showing the well-marked cuticular layer bearing the superficial tomentum, and the broad context bearing the hymenial region.

Fig. 17. *S. Murrayi.* Vertical section through the lower part of the context, showing the subglobose vesicular cells.

Fig. 18. *S. versiforme.*

Fig. 19. *S. sanguinolentum.*



OVERHOLTS: STEREUM

showing a distinct tomentose layer, a definite narrow cuticular layer, and a broad context layer of practically colorless hyphae 3–4μ diameter, septate, compactly and horizontally arranged; spores subcylindric, smooth, hyaline, 5–7$\times$2.5–3μ; cystidia none; with thick-walled hyphae in the basidial layer or in the subhymenial region and these traceable far back into the context.

On dead wood of deciduous trees, especially *Quercus*. This is a common and somewhat variable species, in general reaching larger sizes than most of the others. The species is important as a slash decay fungus working on the slash of large diameter. There are 95 collections in our herbaria from 19 states reaching from Maine to California and in Quebec and Ontario. Burt reports it from 38 states.

8. *Stereum frustulosum* (Pers.) Fr. (fig. 27)

Sporophores closely crowded on the substratum and forming a hard layer that appears to be broken up into units that are angular in shape, 1–6 mm. diameter, appearing as a layer of mud that has cracked into a multitude of small areas, the surface gray to whitish, entirely resupinate, separating into individual dry hard units; in structure typically about 1 mm. thick (occasionally 5–10 mm. thick), composed of erect closely compacted hyphae that are difficult to make out, more or less in annual layers; spores ellipsoid, smooth, hyaline, 5–6$\times$3–4μ; bottle-brush paraphyses abundant in the hymenial region but not conspicuous, 4–5μ diameter.

On logs and stumps of *Quercus* and *Castanea*. Throughout the year. This is a common species, producing a pocket-rot of the wood in which the pockets are lined with white cellulose fibers. It inhabits the lower surfaces of logs in quite dry situations. Specimens are at hand from Nova Scotia, New Jersey, Maryland, North Carolina, Florida, Louisiana, Arkansas, Oklahoma, Missouri, Ohio and Indiana.

9. *Stereum fuscum* (Schrad.) Quel. (fig. 5)

Sessile, usually overlapping, sometimes much effused-reflexed, 0.5–2 cm. long, 2–5 cm. or more broad, uniformly tobacco-brown, more or less zonate and apparently renewing marginal growth yearly, compactly matted-tomentose, thin and flexible when fresh, drying brittle; hymenium white or isabelline, often pruinose-tomentose; in section 400–1200μ thick, no definite cuticular

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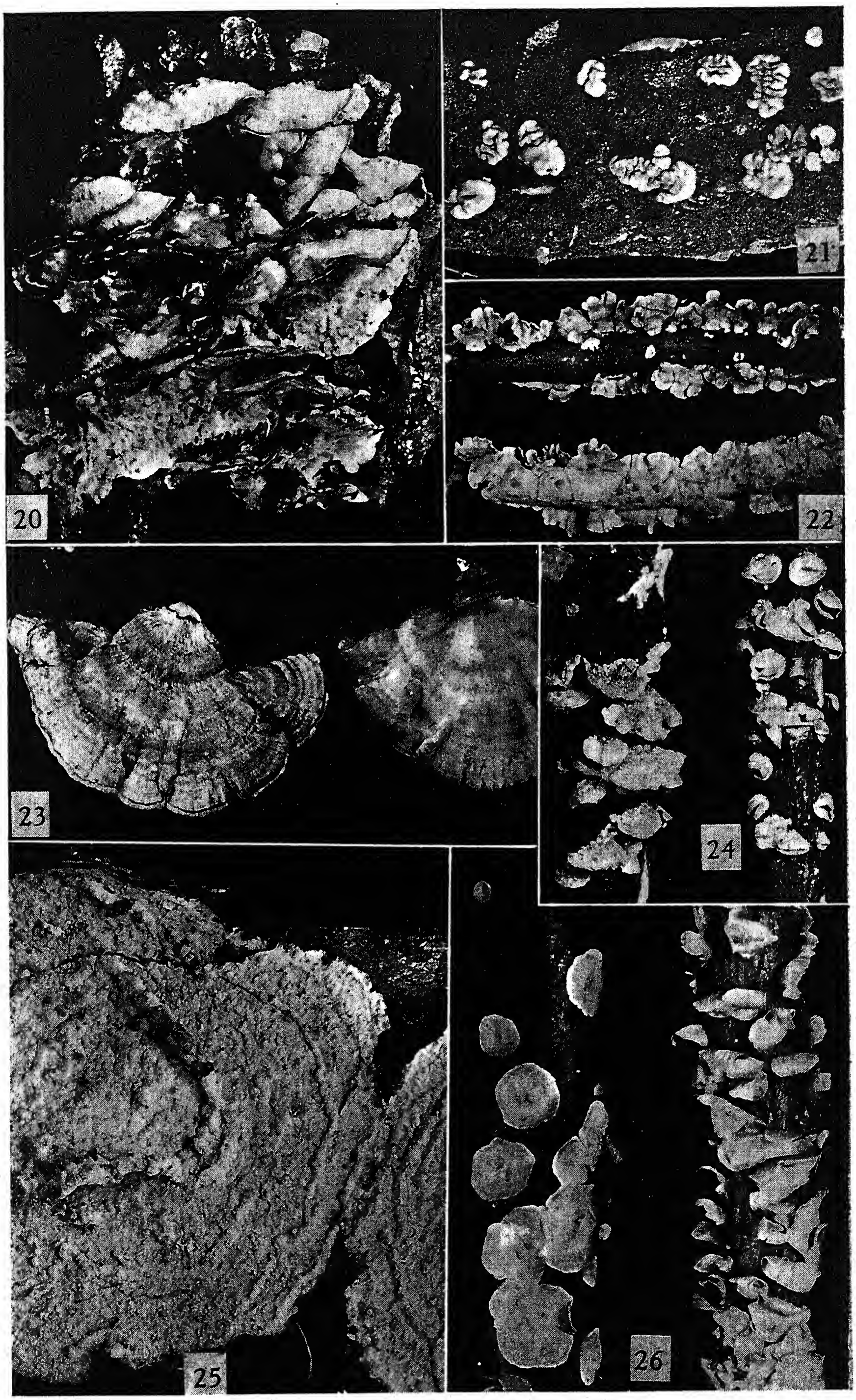
Explanation of Plate 17

Fig. 20. *S. purpureum.*
Fig. 21. *S. rufum.*
Fig. 22. *S. rameale.*
Fig. 23. *S. hirsutum.*
Fig. 24. *S. ochraceoflavum.*
Fig. 25. *S. sulcatum.*
Fig. 26. *S. sericeum.*



OVERHOLTS: STEREUM

layer, brownish or blackish-brown except in the hymenial and subhymenial region, composed of loosely arranged hyphae 3–5μ diameter, with clamps in the upper brown portion, the subhymenium of closely compacted hyaline hyphae 3–4μ diameter; spores ellipsoid, smooth, hyaline, 3–5$\times$2–3μ; gloeocystidia as colored elongated organs, imbedded or projecting, tapering toward the apex, some brown in color and with divided content, 5–8$\times$60–100μ.

On dead wood of deciduous trees. Throughout the year. A species easily recognized by the strong color contrast between upper and lower surface, and the thin tomentose pileus. Not common in Pennsylvania. Specimens are at hand from Ontario, Vermont, New Jersey, Maryland, Virginia, North Carolina, Georgia, Florida, Louisiana, Arkansas, Tennessee, Kentucky, Ohio and Indiana.

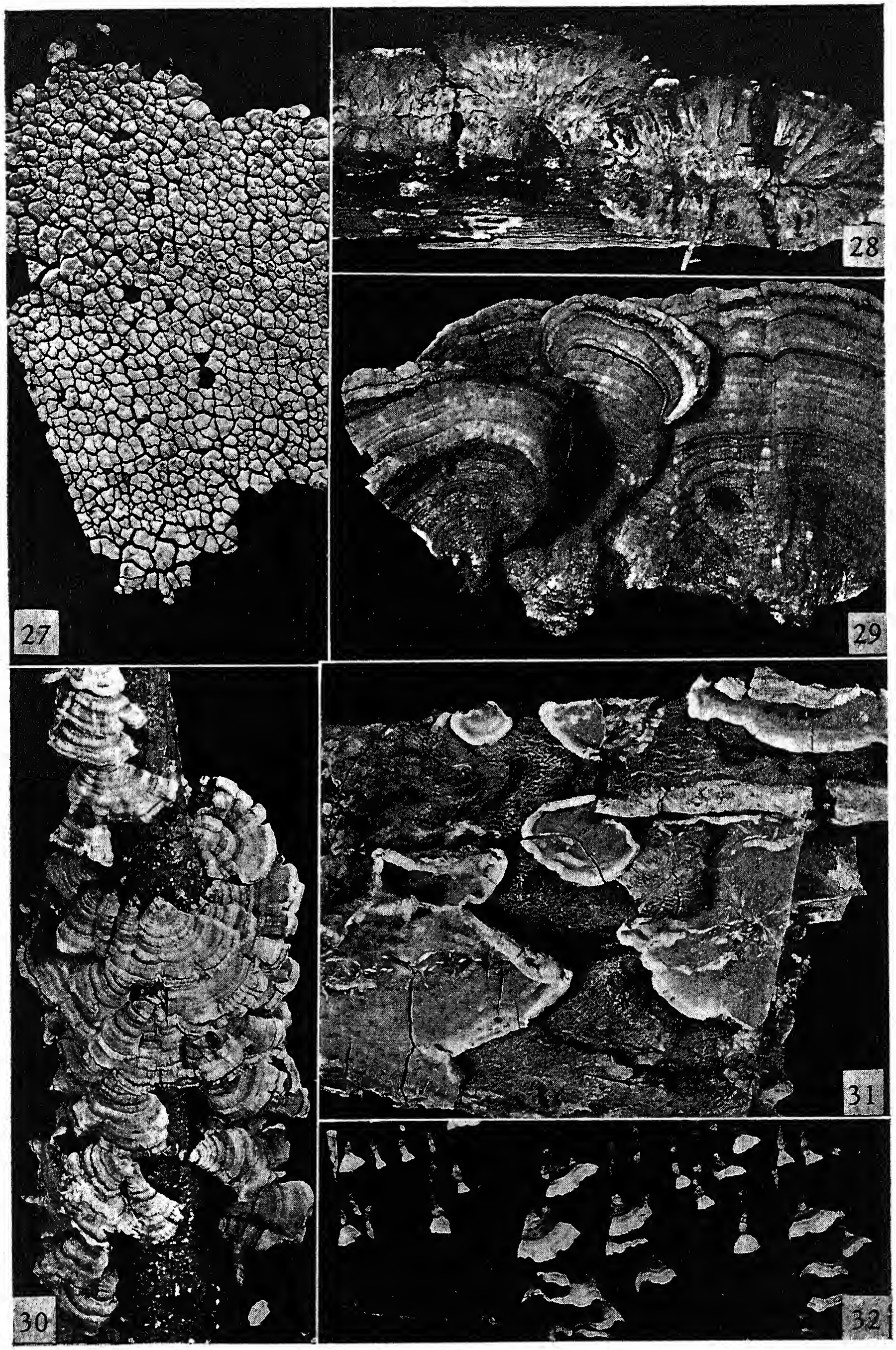
10. *Stereum gausapatum* Fries (fig. 4)

Sessile or effused-reflexed, tough and pliant when fresh, rigid when dry, overlapping, 0.5–2 cm. long, 1–2 cm. broad or laterally confluent to greater sizes, 0.75–1.5 mm. thick, pale yellowish-brown, hirsute, zonate or subzonate, usually crisped or folded; context pallid to smoky or pale brownish; hymenial surface smooth, pale brown and discolored darker on drying, the surface becoming dark reddish where wounded in fresh plants; in section 600–1000μ thick exclusive of the tomentose layer, the broad body of the context bordered on the upper side by a narrow cuticular layer 30–50μ broad supporting the broad tomentose layer, of compactly interwoven hyphae that are hyaline or somewhat colored, thick-walled, 4–7μ diameter; spores cylindric, smooth, hyaline, 6.5–7.5$\times$3μ; colored conducting hyphae usually abundant in the hymenial and subhymenial regions, 5–7μ diameter, best seen in unstained sections.

On dead wood of deciduous trees, especially *Quercus*. This is one of the commoner species in Pennsylvania, especially on the sides of oak stumps not long cut, on which it grows profusely. It has lately been shown that it is the cause of an extensive and destructive heart-rot of living trees. The species is to be distinguished from *S. fasciatum* by the more densely hirsute and thicker pilei, while microscopically the presence of abundant colored conducting hyphae in the hymenial region is an important diagnostic point. Additional specimens are at hand from Connecticut, New York, New Jersey, West Virginia, North Carolina, Louisiana, Arkansas, Tennessee, Oklahoma, Missouri, Ohio and Manitoba.

Explanation of Plate 18

Fig. 27. *S. frustulosum.*
Fig. 28. *S. radiatum.*
Fig. 29. *S. fasciatum.* Unusually larger sporophores.
Fig. 30. *S. rameale.*
Fig. 31. *S. cinerascens.*
Fig. 32. *S. rameale.*



OVERHOLTS: STEREUM

11. *Stereum hirsutum* (Willd.) Fr. (figs. 16, 23)

Sessile or effused-reflexed, tough and pliant when fresh, rigid on drying, hirsute or strigose, gray, zonate in larger specimens, 1–2 cm. long and broad or more narrowly reflexed; context pallid to brownish; hymenial surface pallid, in age gray-smoky; in section 450–1000μ thick (exclusive of tomentose layer), with a definite cuticular layer and a broad context with the main hyphae thin-walled and 4–5μ diameter, but in the subhymenial region with many thick-walled hyphae 5–8μ diameter that make up the hymenial region in young specimens and may contain a yellowish content; spores ellipsoid, smooth, hyaline, 5–7$\times$2.5–3μ; cystidia none.

On dead wood of deciduous trees, usually on the smaller twigs and branches. Common in Pennsylvania. The species is to be distinguished from *S. fasciatum* by the hirsute pubescence, and from *S. gausapatum* in the lack of any considerable number of colored conducting hyphae, though in young specimens some of these structures may be present. The hymenium of this species does not discolor reddish where wounded as in *S. gausapatum,* but this point can only be verified in young growing plants. The general coloration here is gray on the pileus, while in *S. gausapatum* it is more brown or tan. Specimens are at hand from sixteen other states from Maine to Texas and California, and from Quebec, Ontario and British Columbia.

12. *Stereum Murrayi* (Berk. and Curt.) Burt. (figs. 2, 17)

Usually resupinate and widely effused, occasionally narrowly reflexed with a pileus as much as 1 cm. long and 1–5 mm. thick, uniformly coffee-brown then black, soon glabrous, zonate, hard and corky in texture; resupinate specimens usually with a narrow white swollen margin, the hymenial surface white or dirty-white, or in age darkening, typically much cracked into areas 2–5 mm. diameter and these with smaller cracks that break the surface into areas about 1 mm. diameter, usually rugose and uneven; in section not less than 500μ thick and usually much thicker, nearly colorless, without a cuticular layer, the context composed of densely interwoven hyphae about 2μ diameter along the substratum, 3–4μ above, and of many vesicular bodies of ovoid form 15–20$\times$10–12μ, easily visible in crushed mounts; spores ovoid-ellipsoid, smooth, hyaline, 4–5$\times$2.5–3μ; cystidia none.

On dead wood of deciduous trees but especially common on *Betula* and *Ostrya.* A common species in the mountainous regions of Pennsylvania, the favorite habitat being an old birch log. The hymenium is so rugose that the species is likely to be referred to the Hydnaceae. The abundant vesicular bodies are quite conspicuous if fairly thin sections through the sporophore are examined microscopically. Additional specimens are at hand from Quebec, Ontario, New Hampshire, Vermont, New York and West Virginia.

13. *Stereum ochraceoflavum* Schw. (fig. 24)

Sessile or effused reflexed, often thin and conical but typically dimidiate, 2–7(–10) mm. broad and long, white or gray, soft-hirsute or hirsute-tomentose; hymenial surface typically yellow to buff, in age more grayish; in section 200–300μ thick (exclusive of the broad tomentose layer), composed of compactly and horizontally arranged hyphae 3–4μ diameter, with an inconspicuous cuticular layer not well differeniated; hymenial layer composed of basidia and an inconspicuous type of cystidium scarcely broader than the basidia and projecting only slightly, at times their tips minutely mucronate; spores cylindric, smooth, hyaline, 6.5–7.5$\times$2–3μ; no colored conducting hyphae.

On twigs and small branches of deciduous trees. A common species in Pennsylvania, typically easily recognized on its small size, the bright colored hymenium, and the white hairy pileus. It differs further from *S. hirsutum* in the thinner pileus, the much less definite cuticular layer (in section), and in the inconspicuous cystidia. It is especially common on small shrubs in fire-swept areas. Additional specimens are at hand from Ontario, New Jersey, North Carolina, Florida, Georgia, Louisiana, Tennessee, Kentucky and Minnesota.

14. *Stereum Pini* Fries (fig. 3)

Resupinate but finally with the margin free and attached only at the center, at first appearing as small orbicular patches 2–5 mm. broad, with a white fimbriate margin, then enlarging and thickening until the patches are 5–10 mm. diameter; hymenium at first pallid, soon dark gray or drab with a tinge of smoky lavender, finally avellaneous or darker; in section colorless or somewhat yellowish, 160–500μ thick, with a denser cuticular black narrow layer next the substratum, otherwise homogeneous, of closely compacted hyphae running vertically toward the center of ths sporophore but at the margins more horizontal, the walls somewhat gelatinously modified, this region containing some imbedded incrusted cystidia in the central part of the sporophore, and with scattered or rather numerous pyriform vesicular cells, these 15–36$\times$10–16μ; incrusted cystidia also in the basidial layer, numerous or rare, projecting up to 20μ, the incrustation slowly dissolving in KOH, 25–50$\times$5–10μ; spores cylindric or allantoid, smooth, hyaline, 5–7$\times$1–2.5μ.

On dead limbs of sapling *Pinus strobus* and occasionally on other species of *Pinus*. Rather common in central Pennsylvania, especially on small dead branches of saplings in pine plantations. The hymenium sometimes becomes somewhat pruinose and tuberculate under a lens, and specimens of that character were the basis for *Phlebia cervina* Overh. Apparently not a common species. Burt recorded its occurrence in but two states, Maine and New Hampshire. I have additional collections from Quebec, Ontario, Massachusetts and New York.

15. *Stereum purpureum* (Pers.) Fries (fig. 20)

Sessile or effused-reflexed, often imbricate, 0.5–3 cm. long and broad, often laterally confluent, up to 2 mm. thick, coriaceous when fresh, drying rigid and brittle, tomentose or villose-tomentose, with one or two concolorous zones, white to gray or avellaneous; hymenium dirty lavender to smoky-purple or in age smoky-isabelline, even; in section showing a fairly well differentiated cuticular layer, a broad tomentose layer typically thicker than the remainder of the section (1000–2000μ thick), and a broad dense context 500–800μ thick, the upper portion of the context layer loosely arranged, of more open hyphae 4–5μ diameter that bend into the hymenial region, this region of more open hyphae containing thin-walled pyriform to subglobose vesicular bodies 18–24μ diameter that are easily overlooked; spores cylindric, curved, $5–7\times2–3\mu$; cystidia none.

On dead wood of various deciduous trees; perhaps occasionally on conifers. A well marked species, recognized by the typically purplish or smoky-purple hymenium coupled with a tomentose rather than hirsute pileus covering, and with vesicular bodies in the context. The tomentose layer reaches greater thickness than in any other species. This is the fungus to which is accredited the disease known as "silver leaf" that affects various species of trees, especially fruit trees. It is fairly common in Pennsylvania, and specimens are also at hand from Ontario, Maine, Vermont, Massachusetts, Connecticut, New Jersey, Virginia, Indiana, North Dakota, Washington and Oregon.

16. *Stereum radiatum* Peck (fig. 28)

Usually entirely resupinate but occasionally with a narrowly reflexed pileus that is blackish and velutinous on the upper surface, rather thick and coriaceous or somewhat cartilaginous; hymenium dark-brown to blackish-brown, typically with radiating ridges from the center, otherwise even; in section 400–500μ thick exclusive of the tomentose layer, brownish with a red tinge in lactic acid, becoming quickly green and finally decolorized in the hymenial region in KOH, with a cuticular layer, and a tomentose layer about as broad as the context layer that is composed of interwoven hyphae 3–4μ diameter, with clamps; spores cylindric, in age distinctly brown, $7.5–9.5\times3\mu$; cystidia none.

On old coniferous wood, especially structural timbers. The species is rare in Pennsylvania, a total of five collections having been made. It is easily recognized by the brown hymenium with radiating ridges, the color change in KOH, and the largely resupinate habit. The color is rather unusual in *Stereum* and specimens are likely to be referred tentatively to Hymenochaete. Additional specimens are at hand from Quebec, New Hampshire, Michigan and Alberta.

17. *Stereum rameale* Schw. (figs. 8, 22, 30, 32)

Sessile or more often effused-reflexed and sometimes only narrowly pileate, if sessile usually fixed by a point and fan-shaped, spathulate, or dimidate in outline, reflexed sporophores more broadly attached, sometimes laterally confluent, 0.5–1 cm. or slightly more broad and long, thin and coriaceous when fresh, rigid when dry, the color an indefinite gray-cinnamon-buff, becoming more hazel as the thin layer of radiating fibers wears away, usually a bit strigose at the base, the margin often strongly crisped and folded, zonate and more conspicuously so with age; hymenium cinnamon-buff to ochraceous-orange; in section 300–750μ thick (exclusive of the tomentose layer), with a conspicuous cuticular layer under the pileus surface, the hyphae compactly arranged; spores cylindric, smooth, hyaline, $4–7 \times 2\mu$; a few inconspicuous colored conducting hyphae are usually present in the hymenial layer; cystidia none.

On dead wood of deciduous trees, usually on rather small twigs and branches. A common species in Pennsylvania, usually easily recognized by the small size, the zonate and fibrillose-striate pileus that becomes bay or hazel in age, and the fairly bright-colored hymenium. From *S. ochraceoflavum* with which it agrees in size it is to be distinguished by the less conspicuous pileus covering, the more zonate pileus, and the typically less brightly colored hymenium. It is one of the important slash decay fungi in the deciduous forest. Burt reports it as occurring throughout the United States and I have collections from 18 states from Maine to Georgia and west to Texas and Colorado.

18. *Stereum roseocarneum* (Schw.) Fr. (fig. 10)

Sporophore typically resupinate, sometimes with a narrow reflexed margin 1–2 mm. wide and this violaceous-gray to pale-buff, tomentose; hymenial surface pale gray-lavender to lilac-lavender but finally fading, usually becoming cracked; in section 300–500μ thick, without a cuticular layer, the context homogeneous, with loosely interwoven, thick-walled hyphae 3–4μ diameter; spores ellipsoid, smooth, hyaline, $6–9 \times 4–6\mu$; cystidia and vesicular bodies none; narrow paraphyses with antlered branching, 1–2μ diameter present between the basidia.

On dead branches of various deciduous trees, or on decorticated wood, fence-rails, etc. The violaceous or lavender hymenial color coupled with the practically resupinate habit is usually enough to identify this fungus, although the branched paraphyses constitute an additional diagnostic feature. Because of the resupinate habit and the lack of a cuticular layer this species will perhaps often be sought in Corticium. It is rather common in Pennsylvania, and other specimens are at hand from Newfoundland, Quebec, New Hampshire, Vermont, New York and Massachusetts.

19. *Stereum rufum* Fries (fig. 21)

Sporophore tuberculose, erumpent, 2–5 mm. diameter, rather waxy-fleshy, 1–2 mm. high, circular in outline, convex to plane; hymenium strongly rugose at maturity, wine-colored to reddish, pruinose at maturity; in section composed of ascending or erect, incrusted, hyaline hyphae 4–5μ diameter, rather compactly interwoven; spores allantoid, smooth, hyaline, 6–7$\times$2–2.5μ; gloeocystidia abundant in the basidial or subhymenial layer, not projecting, filled with a dense granular material, 7–15μ diameter, the apex pointed or obtuse; cystidia none.

On dead *Populus tremuloides*. Not common in Pennyslvania but occasionally collected. One of the easiest of the stereums to recognize once located in the proper genus. It is more or less aberrant in the genus, however, because of its form and the lack of a definite pileus. The species is widely distributed over the northern United States and Canada, and additional specimens are at hand from Ontario, Manitoba, New Hampshire, New York, Vermont, North Dakota, Montana, Colorada and New Mexico.

20. *Stereum rugosiusculum* Berk. and Curt.

Sessile or effused reflexed, 1–2 cm. broad and long, flexible when fresh, usually imbricate and laterally connate, densely hirsute-tomentose, zonate, gray to grayish black; hymenial surface smooth or rugose, smoky-lavender to fleshy-lavender or fleshy-brown; in section 500–600μ thick exclusive of the tomentum, with a tomentose layer, a cuticular layer, and a broad context layer, the latter of thin-walled hyphae with abundant clamps, 3–4μ diameter, with few or many pyriform vesicular cells imbedded in the subhymenial region; spores cylindric, hyaline, 5–6$\times$2.5–3μ; cystidia scattered, cylindric, hyaline, sometimes slightly incrusted, 4–6μ diameter, projecting 20–40μ.

On dead wood of deciduous trees; occasionally on coniferous wood. Not common in Pennsylvania. From *S. purpureum* this species differs mainly in the presence of cystidia. Widely distributed in the United States. Additional specimens are at hand from Vermont, New Jersey, Idaho and British Columbia.

21. *Stereum rugosum* (Pers.) Fries (fig. 9)

Typically resupinate, sometimes narrowly reflexed and with pileus whitish to gray and sulcate, pubescent to hirsute, becoming glabrate, 1–10 mm. long and broad when reflexed; hymenium cream-color or with livid tinge, changing to red when wounded, darkening with age, even, sometimes slightly cracked on drying, in section 400–800μ thick, with a cuticular layer, the context hyphae densely interwoven, 4–5μ diameter, thick-walled, more or less colored in age, the hymenial region soon layered by perennation, though the layers usually indistinct, each with numerous colored conducting organs 4–6μ diameter; spores cylindric, 6–10$\times$2.5–4μ; cystidia none.

On dead wood of deciduous trees; occasionally on conifers. A species easily confused with *S. gausapatum* and *S. sanguinolentum,* from both of which it is presumed to be distinct in the two-many layered hymenium. The color and pubescence is scarcely that of either species. Rare in Pennsylvania. Additional specimens are at hand from Newfoundland, Quebec and New Hampshire.

22. *Stereum sanguinolentum* Alb. and Schw. (figs. 15, 19)

Sessile or effused-reflexed, coriaceous when fresh, 2–10 mm. broad and long, gray, villous or silky-tomentose, azonate; in section 350–500μ thick exclusive of the tomentose layers, with a narrow but definite cuticular layer and a broad context, the latter often brownish in color, composed of horizontally arranged hyphae 3–3.5μ diameter, and in the subhymenial region with few to many dark-brown conducting hyphae 4–6μ diameter that end between the basidia; hymenium gray to smoky, when fresh exuding a red juice or discoloring red where wounded, even; spores cylindric, hyaline, 5–8$\times$2–3.5μ; cystidia none.

On dead wood of coniferous trees, usually of *Tsuga,* occasionally on others. Rather common in Pennsylvania. This species causes a serious decay of hemlock. Additional specimens are at hand from Newfoundland, Quebec, Ontario, Maine, Vermont, New Hampshire, Massachusetts, New York, Tennessee, Colorado, Idaho and British Columbia.

23. *Stereum sericeum* Schw. (figs. 11, 26)

Sessile or effused-reflexed, typically attached by a point and spathulate to fan-shaped in outline, very thin and coriaceous when fresh, 1–1.5 cm. broad and long, or smaller, whitish or gray, silky with minute radiating fibrils, not folded nor crisped; in section 200–300μ thick, no cuticular layer and no definite tomentose layer, composed of densely arranged horizontal hyphae 3–4μ diameter; hymenium smooth, pallid to wood-color; spores subcylindric, smooth, hyaline, 6–8$\times$2.5–3μ; cystidia and colored conducting organs none.

On dead wood of *Carpinus;* rarely on other substrata. The species is very common on *Carpinus* in Pennsylvania. It can be recognized usually by the substratum, the pallid pileus marked with minute radiating fibrils and very thin. It differs from *S. fasciatum* internally in the lack of cuticular and tomentose layers. Additional collections are at hand from Ontario, New York, New Jersey, Tennessee, Georgia, Florida, Ohio and Indiana.

24. *Stereum subpileatum* Berk. and Curt. (fig. 12)

Resupinate, sessile, or effused reflexed, pileus 0–3(–5) cm. long, 1–4 cm. wide, 1–2(–4) mm. thick, hard and rigid, the surface concentrically sulcate and zoned with narrow zones that finally become glabrous and blackish, tomentose, brown, with a rather distinct black line representing the cuticular layer

under the tomentum; hymenium even, bright cinnamon to somewhat buff, in section 1000μ or more thick, with a broad tomentose layer, a black cuticular layer, and a broad context layer, the hyphae of the latter densely and horizontally arranged, 3–4μ diameter, bearing the hymenium which becomes layered by perennation; spores ellipsoid, smooth, hyaline, 4–5$\times$2.5–3μ; cystidia present, cylindric, incrusted, 6–8μ diameter, in the older layers becoming somewhat brownish, and indistinct, the incrustation dissolving in KOH; paraphyses of the bottle-brush type, sometimes few and indistinct, 3–5μ diameter.

On dead and down logs of *Quercus* and more rarely on other substrata, particularly *Liquidambar*. In its substrata it produces a pocket type of heart-rot similar to that caused by *S. frustulosum*. The fungus reaches its northern limit of distribution in southern Pennsylvania. I found it to be abundant in Louisiana on both *Quercus* and *Liquidambar*. The rotted wood when freshly opened up has a sweet honey-like odor and the fungus in culture is decidedly odorous. *S. sepium* Burt is certainly a synonym and *S. insigne* Bres. has been referred to synonym here. The more abundant the cystidia the fewer the paraphyses that are present, and vice versa. Additional specimens are at hand from New York, New Jersey, Florida, Louisiana, Arkansas, Tennessee and Missouri.

25. *Stereum sulcatum* Burt. (fig. 25)

Entirely resupinate or with a narrow blackish reflexed pileus or a tumid margin, coriaceous or leathery in texture, drying rather hard; hymenium typically with a beautiful ruddy tinge when fresh and becoming darker red where bruised if in fresh condition, roughened and tuberculate and sometimes with concentric ridges; in section 600–1000μ thick (more over the tubercles), more or less colored, with a tomentose layer, a narrow dark cuticular layer, and a slightly colored broad context layer of closely woven and subhorizontal hyphae 2.5–4μ diameter, the hymenial region becoming stratified by perennial growth and the elements there erect and very compact; spores broadly ellipsoid or subglobose, smooth, hyaline, 5–6$\times$4–5μ or 4–5μ diameter; cystidia numerous, imbedded in the tissue or somewhat projecting, incrusted, 25–40$\times$7–12μ.

On dead wood of coniferous trees. This species is rather common in the mountainous region of central Pennsylvania. There is some resemblance to *Stereum Murrayi* but the ruddy hymenium, the presence of cystidia, and the absence of vesicular cells in the context, as well as the coniferous substratum, furnish ample diagnostic characters. Specimens are at hand from Ontario, New Hampshire, Tennessee, Colorado and Idaho.

26. *Stereum umbrinum* Berk. and Curt. (fig. 7)

Resupinate or becoming only slightly reflexed with pileus less than 1 cm. long but nearly always entirely resupinate with a paler margin, coriaceous,

the hymenial surface lavender or purple when young and growing, soon changing to dark brown, even; in section 300–1000μ thick, homogeneous and without a cuticular layer, composed of loosely interwoven, pale brown hyphae 3.5–4μ diameter, with some cross walls but no clamps; spores oblong or oblong-ellipsoid, smooth, hyaline, 6–7$\times$3.5–4μ; cystidia scattered or rather numerous, only in the hymenial or the subhymenial region, projecting up to 50μ, with a thin incrusting layer, colored slightly brownish except where exposed, 6–10μ diameter.

On dead wood of deciduous trees, especially *Quercus*. A beautiful species when in its prime and then easily recognized, but soon discoloring brownish. The cystidia and the open context hyphae are additional diagnostic characters. Additional specimens are at hand from Connecticut, Virginia, Georgia, Florida, Mississippi, Louisiana, Tennessee, Illinois, Missouri and Iowa.

27. *Stereum versiforme* Berk. and Curt. (fig. 18)

Usually entirely resupinate, occasionally with a very narrow tomentose, brown, reflexed margin 1–2 mm. wide, the hymenial surface dark brown, the margin usually nearly white in young specimens but finally darkening; in section 100–250μ thick, rusty brown, darker or blackish toward the substratum, homogeneous but sometimes with two layers, hymenium composed of two kinds of hyphae, one 3–4μ diameter, dark brown and more abundant in the lower part of the context where the arrangement is nearly horizontal, the other paler, 2–2.5μ diameter and comprising most of the context in the upper part; spores cylindric, curved, hyaline 5–7$\times$2μ; cystidia often rather obscure but present, colorless, heavily incrusted but the incrustation dissolving in KOH, very thick-walled, 50–80$\times$15–20μ, immersed or slightly projecting; brownish branched paraphysis hyphae present in the hymenial region.

On dead wood of various deciduous trees. The species is not common in Pennsylvania. It is best differentiated from *S. albobadium* by the much larger cystidia. In section, exclusive of the paraphyses, it resembles *Peniophora cinerea*. Additional specimens are at hand from Massachusetts, Connecticut, West Virginia, Tennessee and Missouri.

The Development of the Embryo Sac and the Seed of Commelina angustifolia Michx.

R. L. McCollum

(with plates 19 and 20)

De Jussieu (1839) studied the embryos of the Monocotyledonous plants almost a hundred years ago and has given an illustration of an isolated embryo of *Commelina tuberosa* which is very similar to those of other members of this group which have been described since that time.

Among other Monocotyledonous embryos, Solms-Laubach (1878) studied those of *Tradescantia, Tinnantia* and *Heterachtia.* In the two latter genera he found evidence which led him to conclude that their stem tips were terminal in origin, but were more or less displaced to the side of the embryo by the growth of the cotyledon. He also called attention to the structure of the megasporangium, mainly on the authority of Le Maout, Seubert and Gärtner. These investigators had observed the segregation of the endosperm and embryo in the mature seed, apparently independently. The method of this separation was not made clear.

From studies on the Monocotyledons, Sargent and Arber (1915) came to the conclusion that in the young seedlings of hypogeal Monocotyledonous plants, two members are distinguished externally—the cotyledon and the main descending axis. The plumlar bud is concealed within the expanded base of the cotyledon. This expanded base constitutes a sheath protecting the plumule during germination. The apex of the hypogeal cotyledon becomes the sucker, absorbing food from the endosperm. The sucker and the sheath are usually connected by a stalk or "limb" which in some cases may be several inches in length; in other cases it may be very short or absent. They regarded the scutellum of *Avena* as strictly comparable with the sucker of *Tigridia,* and the coleoptile as resembling such sheaths as are present in seedlings of *Tigridia, Crocus Colchicum* and *Elettaria.* In hypogeal seedlings the expanded base of the cotyledon is commonly transformed into a closed cylinder, as is the case in *Arum maculatum* L., *Veratrum nigrum* L., etc. They observed that the stalk of *Commelina coelestris* is bent downward at the point where it joins the sheath. This results sometimes in the formation of a hood over the plumule. In *Elettaria,* the sucker of the cotyledon remains in the seed and is connected with the axis by a fairly long stalk. The sheath extends partly above the insertion of the stalk and partly below it. As the stalk extends to the place of its insertion on the sheath, it lies parallel to it.

Quite recently Miss Boyd (1932) has studied seedlings of *Tinantia fugax*, *Commelina coelestris*, *C. dianthifolia*, *C. graminifolia*, and *Tradescantia geniculata* in some detail and other members of the Commelinaceae less exhaustively, and finds a marked uniformity in the structure of the embryos and their mode of germination. The author finds that *Commelina angustifolia* is very similar to these species in structure and germination.

Suessenguth (1921) has studied the development of the embryo in the Angiosperms, paying special attention to the early development of the stem tip and the cotyledon. Among the Commelinaceae *Tradescantia myrtifolia* was studied. He is of the opinion that the terms "lateral" and "terminal," in reference to the growing points of embryos, should be abandoned and, in their places, we should recognize *either*, those embryos whose original terminal cells form only the cotyledon, while the plumule is formed from lower lying cells (the *Alisma* type); or those embryos whose original terminal cells give rise to the cotyledon wall and the plumula. *Tradescantia*, *Tacca* and apparently also *Potamogeton*, *Ruppia*, *Zannichellia* and *Naias* are given as examples of this latter group.

Concerning the development of the gametophyte in the group, Guignard (1882) reported the megaspore mother cell of *Commelina stricta* as sub-epidermal. It divides unequally to give a micropylar cell about one-third the size of the inner cell. The outer of the two cells becomes crushed as the chalazal cell enlarges. He regarded the embryo sac as having arisen from this inner cell of the first division of the mother cell. No evidence is presented to support the conclusion that the embryo sac mother cell is sub-epidermal. Although he reports *C. stricta* to be without a parietal cell, from his figures it seems quite probable that he saw the division of the archesporial cell to form the parietal cell and the mother cell and not the first division of the mother cell.

In *Commelinantia Pringlei* (S. Wats.) B. C. Tharp, Parks (1935) was not able to distinguish the spore mother cell from the other nucellar cells until the prophases of the heterotypic division. At this stage a some-

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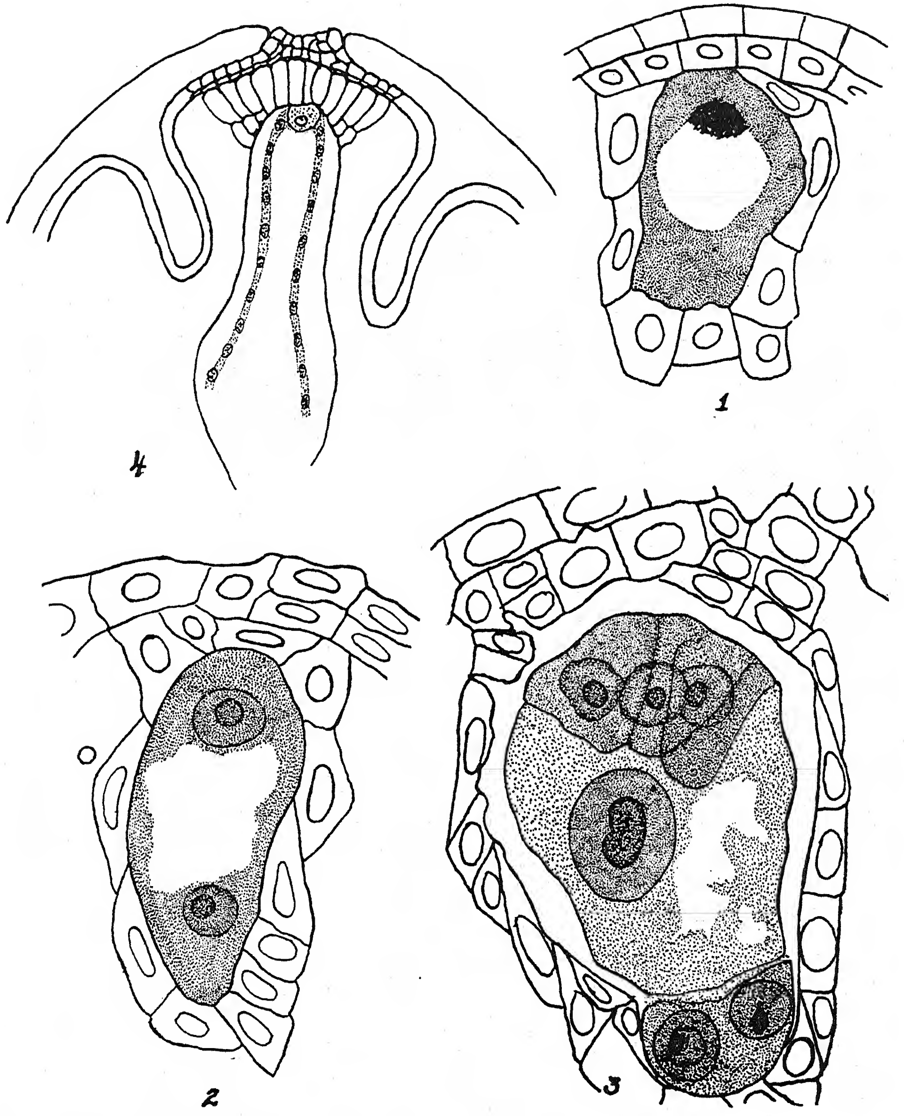
Explanation of Figures

The figures of plate 19 and figure 9 of plate 20 were drawn with the aid of a camera lucida.

Explanation of Plate 19

Fig. 1. Megaspore mother cell in synapsis. ×1300.
Fig. 2. Two-nucleate stage of the mother cell. ×1300.
Fig. 3. Mature 8-nucleate embryo sac; polar nuclei fused. ×1300.
Fig. 4. Fertilized egg stage; endosperm has partly digested the nucellar tissue and has already deeply invaded the chalazal area. ×127.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what flattened cell lies between the megaspore mother cell and the epidermis. After the second division of the mother cell the three outer cells degenerate and the large inner cell divides twice to form a four-nucleate embryo sac.

Commelina angustifolia Michx. grows abundantly in the Austin region. It is found in gardens and waste places throughout the summer. Some stages were obtained also from greenhouse material during the winter.

Strong chrom-acetic fixative and Nawaschin's fluid were used in fixation, the latter being possibly the most satisfactory. The usual technique was followed in embedding in paraffin. Delafield's and Heidenhain's haematoxylin stains were used with equal success. Ripe seeds were embedded in celloidin and sectioned with the aid of a hand microtome at thicknesses of from 30 to 40 microns. Young seedlings with the sucker still surrounded by the endosperm were also embedded in celloidin while others were dissected out of the endosperm before embedding.

The megaspore mother cell is difficult to recognize until it enters into the prophases of the first reduction division. During synapsis it is easily recognized by its large size and the conspicuous cell contents (Pl. 19, fig. 1). A definite layer of cells lies between the epidermis and the other cell,

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Explanation of Plate 20

Fig. 1. Surface view of rounded side of seed. ×7.5.

Fig. 2. An edge of seed showing raphe on upper side and lid on right end. ×7.5.

Fig. 3. End of seed, showing the lid pushed to one side in early germination. ×15.

Fig. 4. Hypocotyl projecting from the seed; raphe shown as elongated line on front surface. ×7.5.

Fig. 5. Tip of hypocotyl turning down in response to gravity; disc-like collar above primary root. ×7.5.

Fig. 6. A somewhat later stage than that in fig. 5. ×7.5.

Fig. 7. A later stage showing four secondary roots coming from the disc. ×7.5.

Fig. 8. The roots are well anchored in the soil at this stage; the upward growth of the limb and sheath has begun. ×7.5.

Fig. 9. An immature embryo lying near the micropyle; section cut at one side of the micropyle. ×42.

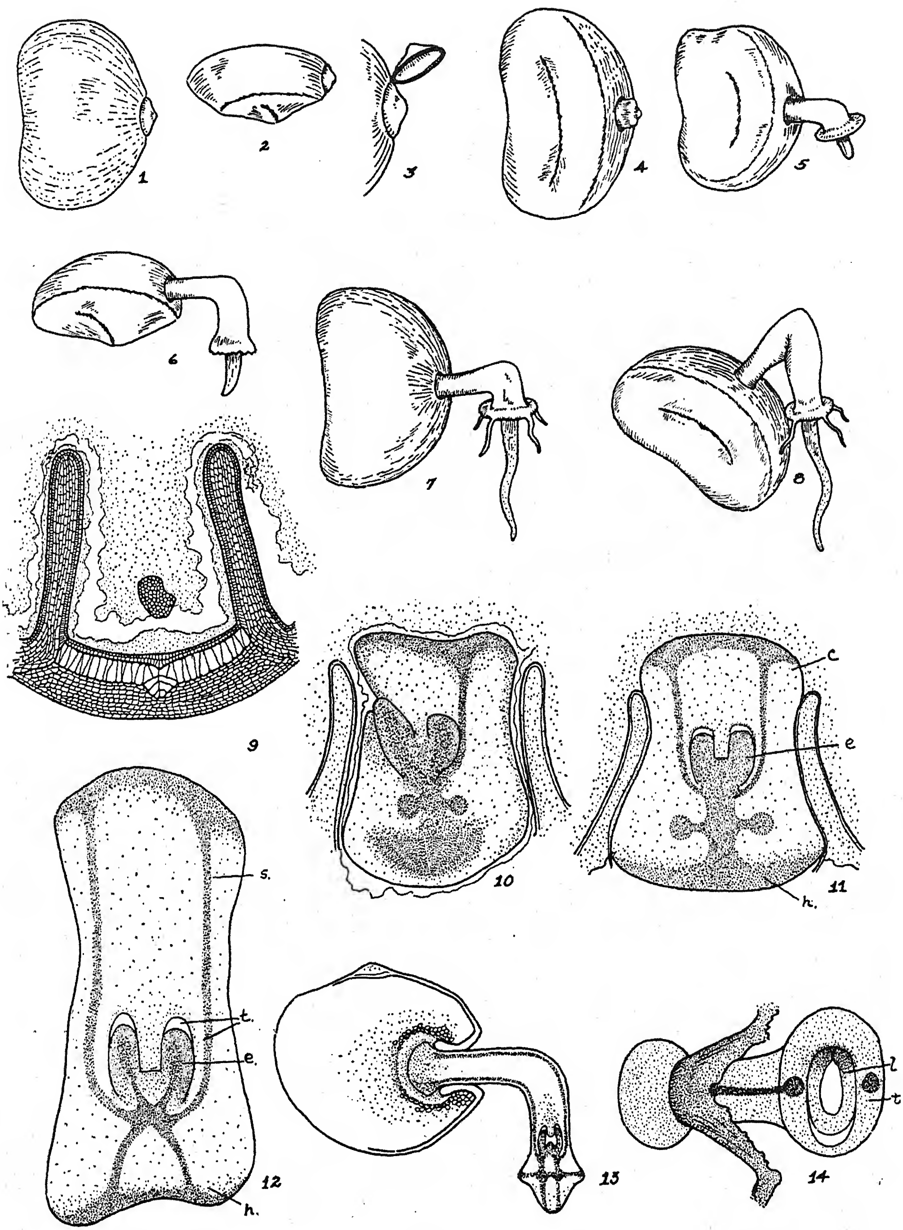
Fig. 10. Embryo nearly mature; cotyledonary tube not fully closed; longitudinal section. ×42.

Fig. 11. Longitudinal section of mature embryo; h. hypocotyl, e. epicotyl, c. cotyledon. ×42.

Fig. 12. A germinating embryo; dissected from the seed; h. hypocotyl, e. epicotyl, t. cotyledonary tube, s. sucker; limb not yet distinct from sucker; longitudinal section. ×42.

Fig. 13. Longitudinal section of seedling and seed; the sucker embedded in the endosperm; apical bud now visible within the cylinder formed by the first leaf. ×11.

Fig. 14. A seedling about the age of that of fig. 7; the section cut parallel to the limb and at right angles to the tube and above the apical bud; the tube is of unequal thickness and encloses the rolled first leaf l. ×20.



McCOLLUM: COMMELINA

and the cell occupying the position of the parietal cell differs little from the others in the layer.

It seems quite certain that all four of the nuclei resulting from the meiotic divisions of the megaspore mother cell, enter into the structure of the embryo sac. The lack of any evidence of walls separating the nuclei, also the lack of any evidence of the disintegration of any of these nuclei, points definitely to the same conclusion.

No stages were observed such as have been reported by Bambacioni (1928), Cooper (1935) and others for certain members of the Liliales in which the three innermost of these four megaspore nuclei undergo fusion after reaching early anaphase, the single mass of chromosomes immediately separating into two masses of chromosomes which then enter into the interphase stage, along with the two nuclei formed normally from the micropylar nucleus.

The development of the megasporangium of *C. angustifolia* is similar to that of *Commelinantia Pringlei* (Parks, 1935). Shortly after the maturity of the embryo sac a constriction is formed immediately back of the antipodal area of the sac by an ingrowing collar-like ring from the outer integument (Pl. 19, fig. 4). This restricts the development of that part of the sporangium adjacent to the micropyle so that very little further growth occurs here. In the subsequent development the growth on the chalazal side of the constriction is very rapid. Fertilization stimulates this growth greatly and it continues to the maturity of the seed. Part of the resulting tissue even surrounds the micropylar part of the sporangium and covers it except at the tips of the integuments at the micropyle. This conspicuous growth is perpendicular to the main axis of the campylotropous ovule and results in a flattened seed convex on one side and nearly plane on the other. A similar development has been described for *Commelinantia Pringlei* (Parks, 1935).

The early development of the endosperm is of the familiar "nuclear" type and naturally is first seen on the micropylar side of the constriction. Later it extends into the tissue on the chalazal side of the constriction which has by this time become many times greater than that of the micropylar part (Pl. 19, fig. 4). The endosperm develops rapidly and finally replaces all the internal parenchymatous tissue of the micropylar side and nearly all that on the chalazal side of the constriction.

In its early phases the young embryo is seen close to the micropyle and partly surrounded by the emdosperm. Somewhat later the embryo shows an asymmetry which is probably due to the early lateral differentiation of the cotyledon (Pl. 20, fig. 9), similar to corresponding stages

figured by Solms-Laubach (1878) for *Heterachtia.* The author has been unable to secure satisfactory views of the growing point of the young embryo and can not say with certainty whether the origin of the cotyledon is the same in *Commelina* as described for *Heterachtia.* When recognizable the epicotyl occupies a central position and remains so to maturity.

As the embryo nears maturity the epicotyl may be seen to have differentiated into the first leaf which surrounds an apical meristem (Pl. 20, fig. 11). The cotyledon has grown upward and surrounds the epicotyl. Occasionally one sees one side of the leaf extended out into the yet unclosed opening through the base of the cotyledon (Pl. 20, fig. 10). However, at maturity this opening is so completely closed that it is difficult to locate its original position. At maturity the stem tip is in the center of an enclosed tube of cotyledonary tissue. (Pl. 20, fig. 11).

As the embryo matures it absorbs the endosperm adjacent to it in the micropylar cavity and completely fills this cavity (Pl. 20, fig. 11). Its upper end, the sucker, extends out into the chalazal area of the sporangium and enlarges to form a slight knob. In the ripe seed the embryo appears remotely dumb-bell shaped, being slightly lobed on each end with a constriction between.

In the dormant condition of the embryo the hypocotyl rests against a disc of tissue formed from the micropylar parts of the integuments. Figure 9 of Pl. 20 shows this disc partly developed. The drawing is from a section cut to one side of the micropyle so that the integuments seem to be covered with the surrounding tissue which is in the background. When the seed is soaked previous to germination the disc is easily displaced by the pressure of the swelling embryo (Pl. 20, fig. 3).

Solms-Laubach (1876) refers to the occurrence of such a disc in *Tinantia, Heterachtia* and other members of the *Commelinaceae.* Hutchinson (1934) mentions it as a "disc-like callosity" of the seeds of the family and calls attention to the use earlier of the terms "embryotega or embryostega" to characterize it (Clark, 1881). Miss Boyd uses the term "lid" in reference to these structures in *Tinantia fugax* (1932).

Two vascular bundles supply the embryo root, two the first leaf of the epicotyl and two the cotyledon. These seem to converge at a region immediately below the epicotyl. At the base of this convergence four bundles branch off which later supply the four lateral roots of the young seedling (Pl. 20, figs. 10, 11 and 12).

The seed is noticeably flattened and is convex on one side and practically flat on the other, which is the side attached to the placenta. This surface shows a long, slightly curved ridge or raphe (Pl. 20, figs. 2 and 4).

The embryo lies at an angle of 90° to the long axis of this ridge. The convex side of the curve of this ridge is toward the position of the embryo (Pl. 20, figs. 4 and 8). The micropyle and "lid" thus appear on the edge of the flattened seed.

In the early stages of germination the cotyledonary region of the embryo elongates and pushes the basal part of the embryo out of the seed coat (Pl. 20, fig. 4). After the hypocotyl has grown out for a short distance beyond the seed, the tip becomes sensitive to gravity and turns down (Pl. 20, fig. 13). A disc-like collar soon forms, apparently at the juncture of the stem and root (Pl. 20, figs. 5, 6, 13). Rapid growth of the tap root follows and four lateral roots form equidistantly on the disc (Pl. 20, figs. 7,8). The seedling, at this stage, when covered with soil is anchored at the one extremity by the "seed" and at the other extremity by the tap and lateral roots. By this time those parts of the embryo between the "seed" and the root disc have already begun to elongate upward (Pl. 20, figs. 7, 8). The parts concerned in this elongation are the cotyledonary limb on the side connected with the seed and the cotyledonary sheath surrounding the epicotyl on the other side (Pl. 20, fig. 8). These must of necessity grow alongside until the plumule breaks out of the sheath at the surface of the ground.

At the base of the sheath, within the cylinder of the first foliage leaf, there is a bud which develops to form the next internode and the second foliage leaf. The meristem at the base of this second leaf repeats this development so that, in a seedling shortly before it appears above the ground there may be several leaves separated by internodes, telescoped one within the other.

The separation of the seed into two distinct regions or compartments, the one containing the embryo and the other the endosperm, seems to have been observed only in the Commelinaceae. At first thought, the early separation from the endosperm may appear to be an adaptation to insure the carrying over of abundant endosperm. However the embryos of the Commelinaceae are often as large as those of many seeds in which the embryo is surrounded with endosperm as *Asparagus*, *Smilacina* and other members of the Liliaceae. From these examples it would seem that in the Monocotyledons, embryo size has little relation to its proximity to the endosperm.

Cotyledonary "limbs" which are attached to the top of the cotyledonary tube are not peculiar to the Commelinaceae, but are found in various genera of the Liliaceae. If the seeds of such plants are buried deeply the delicate limb becomes unduly extended upon germination and

must be very susceptible to injury when in this condition. The organic nutrients from the endosperm must pass twice as far to reach the developing root, the hypocotyl and epicotyl as would be the case if the limb was attached to the base of the tube. It is probable that very few seeds of these genera in question are too deeply buried but more often are not buried deep enough so that the normal limb would be very short.

In *Galtonia*, the Alliums, and others of the Liliaceae, the cotyledonary limb normally grows vertically downward, carrying the radicle and plumule deeply into the soil, producing a situation similar to that found in *Commelina* in which the organic food must be transported a considerable distance through a very slender structure. These limbs and their downward growth are very suggestive of the slender "droppers" of the Tulip by means of which the terminal bud is carried deeper into the soil each season. The "dropper" is a slender tubular structure carrying the terminal bud in its tip. Most of the remaining organic food of the last bulblet is transferred to the new bulblet through the vascular system of the dropper. These droppers are scarcely larger than the limbs of Commelinaceae but may be very long, exceeding nine inches (Arber, 1925). Such delicate structures, distinctly different in their origin, thus are frequently used among the Monocotyledons to protect the stem bud and to supply nutrition when it is being brought to the surface or carried deeper into the soil.

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The Cytology of Apogamy in Pteris cretica Linn. var. albo-lineata Hort.

Alphonse L. Heun

(with plates 21 and 22)

The first evidence of apogamy in a ferm was reported by Lesczyc-Suminski (1848) who observed tracheids in the prothallium of *Pteris sulcata.* Later Wiegand (1849) in some mixed fern cultures found prothallia which produced at the apical notch conical processes bearing embryos, which were, no doubt, of apogamous origin. Mercklin (1850) also found tracheids in the prothallium of *Pteris sulcata* and figured a gametophyte of a fern, probably that of *Notholaena Eckloniana,* with a sporophyte of apogamous origin.

Farlow (1874) clearly described for the first time the phenomenon of apogamy in a fern, in *Pteris cretica* var. *albo-lineata,* in which he observed that the apogamous embryo is an asexual growth from the ordinary prothallial cells. The first evidence of the apogamous embryo, according to Farlow, was the appearance of a pale green region in the gametophyte immediately back of the apical notch, in which tracheids later on developed. Frequently there was formed a process similar to that described by Wiegand (1849) from which an embryo was often observed to develop, usually on the ventral side of the prothallium just posterior to the process. The leaf of the embryo appeared first, then the root and finally the stem. The foot was always absent. De Bary (1878) also investigated the origin of the embryo of *Pteris cretica* var. *albo-lineata* and found it to be constantly apogamous.

Since the investigations of Farlow (1874) and De Bary (1878) apogamy has been discovered in numerous ferns and has been studied by many botanists including: Hayes (1924), Heilbronn (1910), Heim (1896), Kny (1895), Lang (1898, 1924, 1929), Leitgeb (1886), Nagai (1914), Pickett and Manuel (1925), Sadebeck (1879), Stange (1887), Sarbadhikari (1939), Steil (1911, 1915, 1918, 1919, 1933), Woronin 1907, 1908) and Yamanouchi (1908b).

Only a few cases of apogamy have been cytologically investigated. Farmer, Moore and Digby (1903) reported that in the gametophyte of *Lastraea (Dryopteris) pseudo-mas* var. *polydactyla* (Wills) and in *Lastraea (Dryopteris) pseudo-mas* var. *polydactyla* (Dadds) there occurred first a fusion of two vegetative cells and their nuclei. According to their description, the diploid apogamous sporophyte originated from the

cell resulting from these fusions. Binucleated cells have been reported in the prothallia of other ferns by Lang (1898) and Hayes (1924), but these cells never produced apogamous sporophytes. Miss Hayes also found "fusion" nuclei in the gametophyte of *Pellaea atropurpurea.* Stephens and Sykes (1910) described binucleate cells in the gametophyte of *Pteris droogmantiana.* They showed, however, that this nuclear condition resulted from a mitotic division which was not followed by cell division.

Miss Digby (1905) found that in *Nephrodium* (*Dryopteris*) *pseudo-mas* Rich. var. *cristata* there occurred no reduction division. The diploid number of chromosomes was found in both the gametophyte and the sporophyte generation. Farmer and Digby (1907) studied the chromosome number in some apogamous and parthenogenetic ferns. Also, in 1907 they reported a haploid sporophyte in the apogamous *Lastraea* (*Dryopteris*) *pseudo-mas* var. *cristata apospora.* The chromosome numbers in apogamous ferns which have been cytologically investigated are as follows:

	Gametophyte	*Sporophyte*	*Haploid or Diploid*	*Worker*
Athyrium filix-foemina var. *clarissima* Jones ..	90	90	Diploid	Farmer, Digby (1907)
Nephrodium (*Dryopteris*) *pseudo-mas* var. *cristata*	50	50	Diploid	Farmer, Digby (1907)
Lastraea (*Dryopteris*) *pseudo-mas* var. *cristata apospora*	60–78	60–78	Haploid	Farmer, Digby (1907)
Lastraea (*Dryopteris*) *pseudo-mas* var. *polydactyla* Wills.	64–66	128–132	....	Farmer, Digby (1907)
Lastraea (*Dryopteris*) *pseudo-mas* var. *polydactyla* Dadds	64–66	128–132	....	Farmer, Digby (1907)
Nephrodium (*Dryopteris*) *molle*	64–66	64–66	Haploid	Yamanouchi (1908)
Nephrodium (*Dryopteris*) *hirtipes*	60–66	60–66	Haploid	Steil (1919)
Aspidium (*Dryopteris*) *remotum*	130	130	Haploid	Döpp (1932)
Aspidium (*Dryopteris*) *filix-mas* var. *cristata*..	80	80	Haploid	Döpp (1933)
Aspidium (*Cyrtomium*) *falcatum*	60–66	60–66	Haploid	Allen (1911)
Marsilia Drummondi	16 or 32	32	....	Strasburger (1907)
Pellaea atropurpurea ...	40	40	Haploid	Hayes (1924)

Similar fusions of cells were described by Miss Allen (1911) in *Aspidium* (*Cyrtomium*) *falcatum.* According to her description the hap-

loid sporophyte arises from a haploid gametophyte. In the sporangium sixteen sporocytes fuse in pairs and produce eight diploid spore mother cells which produce, in the ordinary way, thirty-two haploid spores. Strasburger (1907) found two kinds of mother cells in the macrosporange of the heterosporous *Marsilia Drummondi.* Some macrospore mother cells of this fern contain larger nuclei than others. The smaller nuclei pass through a typical reduction division to form the normal spores. The larger nuclei, however, Strasburger describes as passing through an apparent synapsis which is followed by no reduction of the chromosome number. Yamanouchi (1908 b) found in *Nephrodium* (*Dryopteris*) *molle* that the prothallia bore both antheridia and archegonia, and that under ordinary conditions fertilization took place, but, if the prothallia were watered only from below and grown in strong light, apogamous sporophytes were produced. Yamanouchi observed no migrations of nuclei as described by Farmer and Digby (1903), but that the haploid sporophyte arose directly from the gametophyte. Miss Black (1909) and Mottier (1915) attempted to produce apogamous embryos in *Nephrodium* (*Dryopteris*) *molle* but failed to obtain them, although as far as possible they used the same culture methods employed by Yamanouchi. Mottier questions the apogamous origin of the embryos described. Steil (1918) also made futile attempts to obtain under cultural conditions similar to those described by Yamanouchi, apogamous embryos of *Osmunda regalis.*

Steil (1919) found in *Nephrodium* (*Dryopteris*) *hirtipes* that a haploid sporophyte arises from the vegetative cells of the haploid gametophyte. When eight sporogenous cells have been produced, they undergo incomplete nuclear and cell divisions, which result in the production of eight spore mother cells with the diploid number of chromosomes. The diploid spore mother cells thus produced undergo the reduction divisions and produce thirty-two haploid spores. Steil (1919) found that similar incomplete ("interrupted") divisions occur in the spore sacs of *Aspidium* (*Cyrtomium*) *falcatum.* Döpp (1932) also found in the spore sacs of the apogamous *Aspidium* (*Dryopteris*) *remotum* incomplete nuclear and cell division similar to those described by Steil. Döpp (1933) also described the same phenomenon in much detail in the apogamous *Aspidium* (*Dryopteris*) *filix-mas* var. *crist.* Hort.

Miss Hayes (1924) investigated the cytology of *Pellaea atropurpurea* and although she found binucleated cells, migrating and apparently "fusion" nuclei she could not trace the origin of the apogamous embryo to fusions of ordinary gametophyte cells. Miss Hayes found forty chromosomes in both gametophyte and sporophyte. Since no fusions or incom-

plete nuclear divisions occurred in the sporogenous cells the reduction divisions failed to take place.

MATERIALS AND METHODS

The spores for cultures were collected in the Marquette University greenhouse and in the Mitchell Park Conservatory at Milwaukee, Wisconsin. The prothallia were grown in Erlenmeyer flasks containing Beyerink's solution as modified by Moore. The cultures were kept in a Wardian case in the greenhouse. Protonema-like filaments were formed in cultures in which the spores were sown very thickly. These filamentous prothallia bore antheridia only. In the cultures exposed to good light normal prothallia developed. The material for cytological study was fixed in Fleming's medium strength fluid or in a modified Navashin's solution. Preparations were stained with the Flemming triple: safranin, gential violet and orange G, and with Heidenhein's iron hematoxylin. Safranin and fast green proved very satisfactory for the counting of the chromosomes. The sections were generally cut 10 microns in thickness. Spore mother cells were counted in serial sections. Spore counts were made both from prepared slides and by removing a mature spore case and placing it into a drop of water on a slide. A cover glass was then placed on the mount and a drop of glycerin was introduced. The counts could then be readily made.

OBSERVATIONS

The Gametophyte

The prothallia of *Pteris cretica* var. *albo-lineata,* when exposed to good light, broaden out and form typical heart-shaped structures. These

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Explanation of Plates

All figures were drawn with the aid of a camera lucida. All except 6 and 16 were drawn at 2650 diameters. Figures 6 and 16 were drawn at 1620 diameters. The figures in Plate 21 have been reduced about one-sixth and those in Plate 22 have been reduced to one-half in the printing reproduction.

Explanation of Plate 21

Fig. 1. A polar view of a vegetative cell of the gametophyte showing the 32 chromosomes.

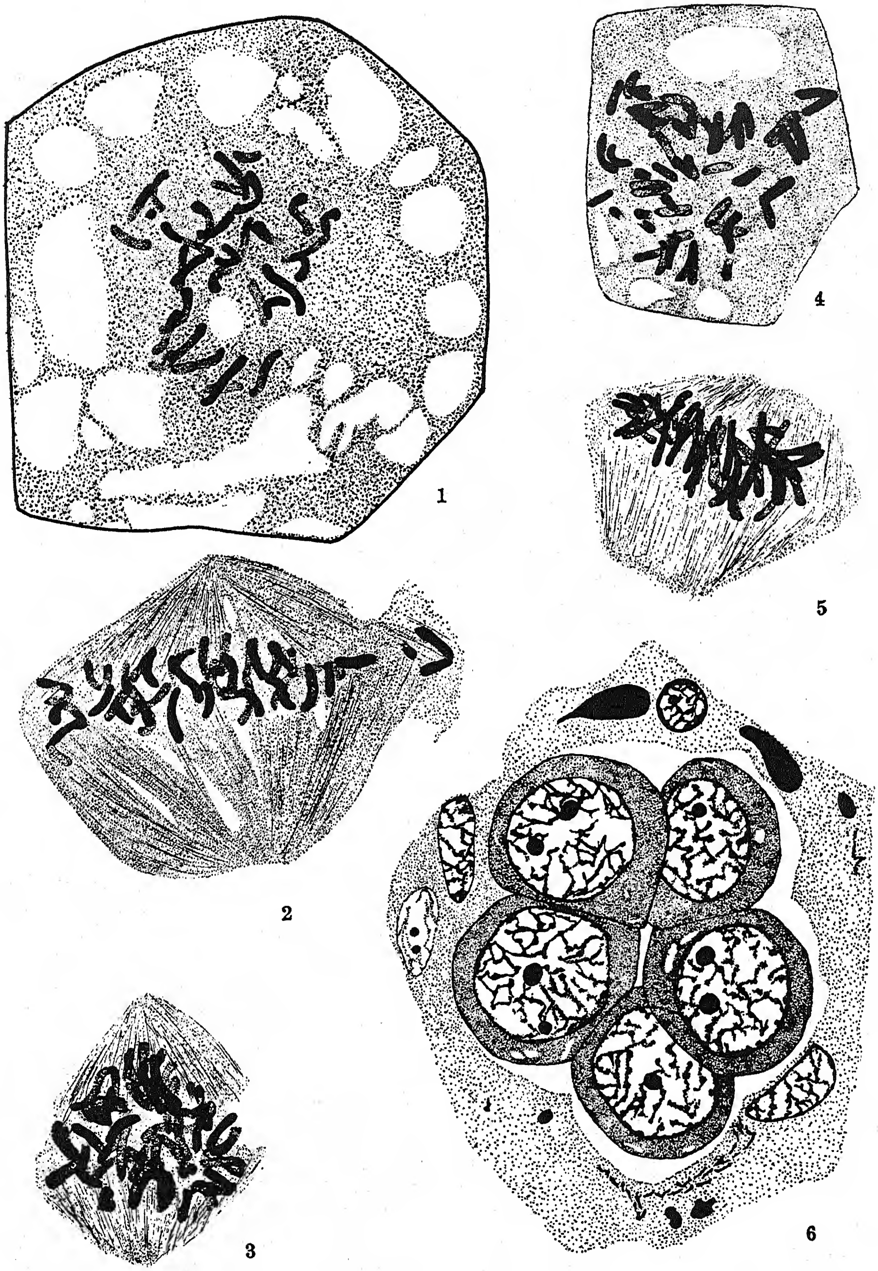
Fig. 2. Longitudinal section through a metaphase of a vegetative gametophyte cell.

Fig. 3. Metaphase of a young sporophyte cell. All of the chromosomes are shown.

Fig. 4. Polar view of a root tip cell in metaphase. There are 32 split chromosomes.

Fig. 5. Metaphase in a cell of a very young sporangium showing the full chromatin content.

Fig. 6. Four of the eight spore mother cells with disintegrating tapetum surrounding them.



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bear rhizoids, antheridia and archegonia. In the cultures practically all of the normally developed prothallia produce archegonia, but the latter are few in number, varying from one to four on each gametophyte. They develop in the normal way producing a definite neck and venter in which an egg is formed. However, the entire contents of the archegone including the egg cell disintegrates.

Mitotic figures were observed in the young antheridia and in the vegetative cells of the prothallia. In polar view during anaphase (fig. 1, Pl. 21) the chromosomes are more or less scattered and the count is readily made. The chromosome number in the nucleus, represented in the figure, as well as in all others in which counts were made, was found to be 32. Figure 2, Pl. 21, shows a longitudinal section through a vegetative cell of the gametophyte. About two-thirds of the chromosomes are represented. This figure shows the broad spindle poles and the chromosomes in the equatorial plate stage. The number, 32, is believed by the writer to be the haploid number which is about half of the number reported in the gametophyte of the common *Dryopteris* species of ferns.

The Sporophyte

The apogamous development of the sporophyte of *Pteris cretica* var. *albo-lineata*, as has been stated, was investigated by Farlow (1874) and De Bary (1878). The author has confirmed, as a result of his studies, the conclusions of these workers.

In the cells of the young apogamous sporophyte the writer counted the chromosomes and the haploid number of 32 was found to be present. In the sporophyte the division figures are comparatively abundant. Figure

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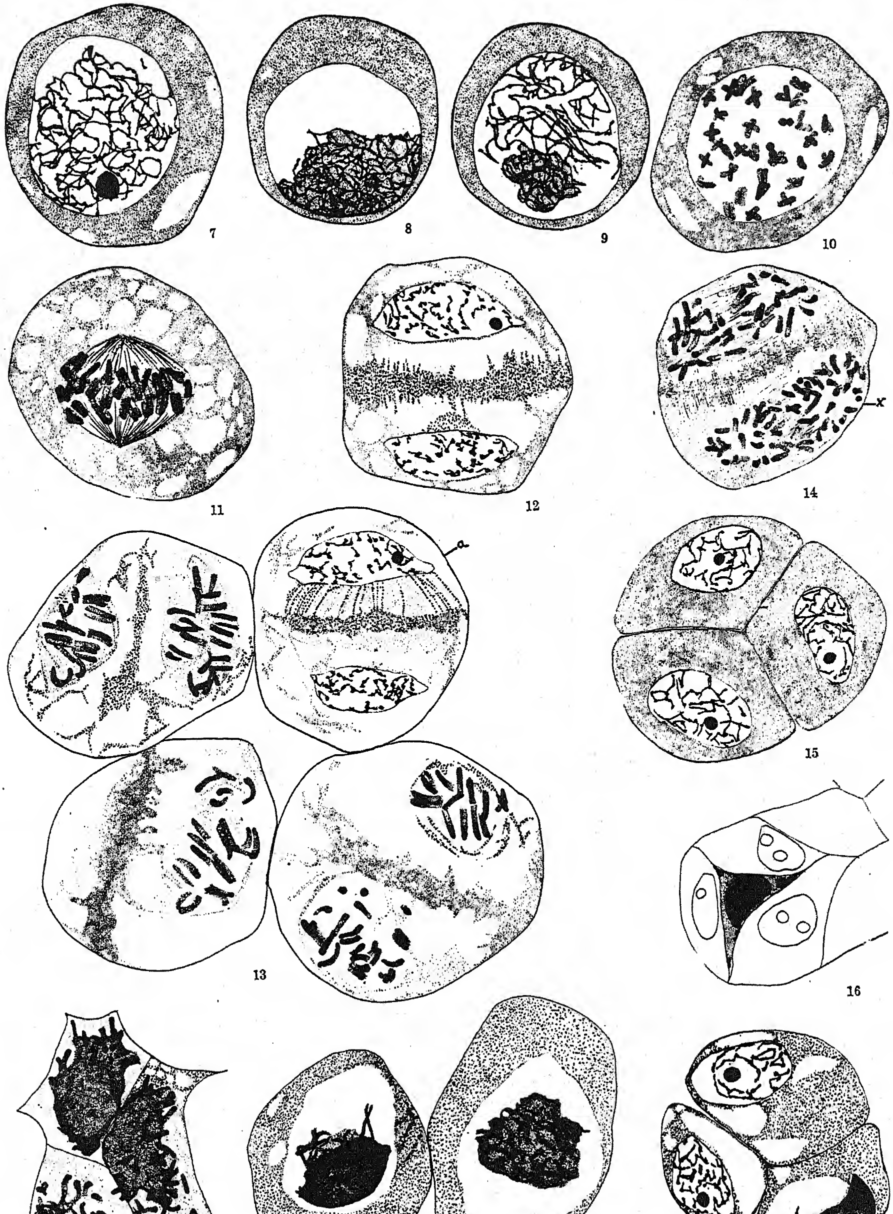
Explanation of Plate 22

Fig. 7. Early prophase in a spore mother cell.
Fig. 8. Pseudo-synapsis in a spore mother cell.
Fig. 9. Leptonema stage showing the longitudinal split of the spireme.
Fig. 10. Diakinesis in a spore mother cell. Thirty-two split chromosomes are shown. This is the entire complement of the cell.
Fig. 11. The first metaphase in a spore mother cell. All of the chromosomes are shown.
Fig. 12. Interphase between the two divisions preceding spore formation. A nucleolus is present in one nucleus.
Fig. 13. A group of spore mother cells, one of which is in interphase, the others in the second metaphase.
Fig. 14. Second anaphase in the spore mother cell, showing at X the 32 chromosomes.
Fig. 15. A tetrad of young normal spores.
Fig. 16. Abortion in the archesporial cell.
Fig. 17. Abortion in sporogenous tissue.
Fig. 18. Abortion in the spore mother cells occurring during synapsis.
Fig. 19. Abortion in young spores.



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3, Pl. 21 shows a metaphase stage in the young sporophyte. The chromosomes can be distinguished readily although, on account of the smaller size of the young sporophyte cells, a more compact arrangement of the chromosomes results and hence they are more difficult to count. In this figure there is shown the complete chromatin complement, consisting of 32 split chromosomes.

The meristematic region of the root tip was studied in longitudinal and transverse sections, and the number of chromosomes counted. A polar view of the metaphase (fig. 4, Pl. 21) of the root tip of a mature sporophyte shows the chromosomes well distributed over a broad plate which extends almost to the cell wall. There are in the nucleus of the root tip cell 32 chromosomes, as represented in the figure.

The Sporangium

The cells of the sporangium in their early stages are larger than those of the root tip and the crozier, which were also studied for the chromosome number. Figure 5 of Pl. 21 shows a cell of a developing sporangium. This cell is only one division removed from the sporangium initial cell. This cell shows 32 chromosomes as represented in the figure. Hence, there has been no change in the number of chromosomes in the life cycle of the fern, the sporophyte having the same number as the gametophyte.

As a result of the study of the tapetum of the spore sac, disintegration of its cells was found to occur at an early stage, the walls of the tapetal cells are first digested and then the tapetal nuclei disintegrate. By the time the eight spore mother cells have been developed, the disintegration of the tapetal cells has been completed (fig. 6, Pl. 21) and their nuclei have begun to break down. The eight spore mother cells shown in this figure are rounded on the sides adjacent to the periphery of the sporangium, and have attained their maximum size. Their cytoplasm is dense and granular. The nucleus is located centrally, is of large size, spherical and deep staining. The chromatin forms a net-like structure, which in no instance is composed of a double thread. Hence, there is no pairing of chromosomes.

In the prophase of the spore mother cells there appears to be, at first glance, a typical sequence of the stages of a meiotic prophase. Figure 7 of Pl. 22 shows such an early stage of the prophase. There has occurred no longitudinal split of the threads the number of which, at this stage, could not be determined. The chromosomes next pass into what appears to be a synaptic knot. In this apparent "synapsis" there is not at any time a pairing of the chromosomes (fig. 8, Pl. 22). Hence, a true synapsis does not take place. The longitudinal split of the threads occurs at the end of

this pseudo-synapsis, and the knot loosens up in a typical leptonema-like stage (fig. 9, Pl. 22). In this stage the threads are thin but show evidence of a longitudinal split. There now occurs a contraction of the chromosomes. There is no tetrad formation at any time in the mitotic divisions. The chromosome pairs are well distributed throughout the nucleus, which has regained its central position within the cell. The cytoplasm of the spore mother cell, at this stage, is more highly vacuolate than in the earlier stages. The chromosomes were counted at this stage in a number of cells and found to be 32 in number. Figure 10 of Pl. 22 shows all of the chromosomes of an apparent "diakinesis." The chromosomes next arrange themselves in pairs upon a rather narrow plate in the center of the mother cell (fig. 11, Pl. 22). The well developed spindle fibers appear to be in groups as shown in the figure. The chromosomes are drawn to the poles by the spindle fibers, all of the split chromosomes being separated and reaching the poles. Evidently a mitotic division of the nucleus has occurred instead of a meiotic division.

At this stage in the development of the spore there ensues a typical interphase (figs. 12 and 13a, Pl. 22), the chromatin passing into the metabolic condition during which time there is produced a nuclear membrane. A second spindle is later formed. Up to this time there has been a complete uniformity in the development of the sporogenous tissue within a single sporangium, although within a sorus one may find various stages of development from sporangium initial cells to sporangia containing mature spores. The individual chromosomes which are longitudinally split can be readily observed in metaphase. The cells represented in figure 13, Pl. 22 show this split condition of the chromosomes. Only a few chromosomes are represented in these cells, the remainder appearing in the adjacent sections of the series. The chromosomes are slightly thinner than those of the previous division but retain their characteristic length and shape. The spindle fibers separate the split halves of the chromosomes and draw them to opposite poles (fig. 14, Pl. 22). Chromosome counts were again made in each of the two dividing nuclei of the spore mother cell, and 32 chromosomes were found to be present.

Spindle fibers are in evidence after the second mitotic division has been completed (fig. 14, Pl. 22). The walls of the spores, at first thin, become quite thick. The four members of the tetrad of spores are not separated at once, and it seems that the secondary thickenings, resulting in the highly sculptured condition of the mature spores, is partially responsible for their separation. The cytoplasm in the young spores is again very dense and not highly vacuolate (fig. 15, Pl. 22), and the nucleus is ap-

proximately in the center of the cell. A nuclear membrane is present and the chromatin appears to form a reticulum. One or more nucleoli have appeared in each nucleus.

Abortion in the Sporangium

Only about 30 per cent of the sporogenous cells of *Pteris cretica* var. *albo-lineata* develop normal spores. The remainder disintegrate at various stages in the development of the sporangium. The earliest evidence of abortion of sporogenous tissue observed by the writer occurred when the primary cell has been differentiated (fig. 16, Pl. 22). The nucleus in the aborted cell stains deeply, and is often an apparently homogeneous mass. In most instances in such disintegrating cells, there are present in the cytoplasm extrusions of chromatin. Several masses of "chromatin" are sometimes visible in the cytoplasm as shown in figure 16 of Pl. 22. Figure 17 of Pl. 22 shows abortion occurring at the four celled stage. It appears ordinarily, as shown in this instance, that disintegration occurs during the time of nuclear division. In the spore mother cells no disintegration was observed during the resting stage of the nucleus. During pseudo-synapsis, disintegration of the nucleus commonly takes place (fig. 18, Pl. 22). In the apparent synaptic stage, the chromatin is reduced to a homogeneous mass. In one cell shown in figure 18 of Pl. 22 the remains of a few chromatin strands can be observed; in the other cell is shown a very early leptonema-like stage. The cytoplasm of the aborted cells at this stage is not of a uniform density throughout, as in the normal mother cells at "synapsis." The nucleus is irregular in outline and frequently its membrane is disappearing, or has completely disappeared. The cell seems to lack turgidity, and is apparently abnormal.

Abortion was also observed in late stages of the spore development, as shown in figure 19, Pl. 22. In this figure a tetrad of spores is undergoing disintegration. The nucleus of one of the spores in the tetrad has been reduced almost to a homogeneous mass. The only remaining distinguishable portion of the nucleus is the nucleolus. The cells are approximately the size of a normal young spore, but they no longer have their characteristic outline. There has appeared a very large vacuole near the nucleus. This large vacuole is also present in another cell of the tetrad, in which the nucleus still retains its reticulum but is irregular in form. This cell represents an earlier stage of disintegration of the spore. In the third cell of the tetrad the nuclear contents are no longer distributed evenly throughout the nucleus. The karyolymph is slightly stained. A shrinking of the nuclear material from the nuclear membrane was frequently ob-

served. Large vacuoles commonly appear in the cytoplasm of the disintegrating spore, as shown in the figure.

The cause of abortion of the sporogenous cells of *Pteris cretica* var. *albo-lineata* is unknown to the writer.

Discussion

In the cultures of prothallia made by the writer, the normally developed gametophytes always produced antheridia and archegonia. The large heart-shaped prothallia were produced when fewer spores were sown in the culture. In this fern there are no cell and nuclear fusions like those described by Farmer and Digby (1907), or Miss Allen (1911). Neither are there incomplete nuclear and cell divisions like those described by Steil (1919) and Döpp (1932, 1933). Furthermore, since there are no reduction divisions in the life cycle, the cytology of the fern is similar to that described by Miss Hayes (1924) in *Pellaea atropurpurea.*

The chromosome number, characteristic of both gametophyte and sporophyte of *Pteris cretica* var. *albo-lineata,* as has been stated, is thirty-two. The writer assumes that this is the reduced number and therefore the sporophyte is also haploid. The haploid condition of the sporophyte in ferns has already been described by a number of workers: Farmer and Digby (1907) in *Lastraea* (*Dryopteris*) *pseudo-mas* var. *cristata apospora,* Yamanouchi (1908 a) in *Nephrodium* (*Dryopteris*) *molle,* Allen (1911) in *Aspidium* (*Cyrtomium*) *falcatum,* Steil (1919) in *Nephrodium* (*Dryopteris*) *hirtipes,* and Döpp (1932) in *Aspidium* (*Dryopteris*) *remotum* and (1933) *Aspidium* (*Dryopteris*) *filix-mas* var. *cristata* Hort. found the haploid number of chromosomes in both generations.

The writer wishes to express his appreciation to Dr. W. N. Steil of Marquette University for valuable advice and suggestions given during the preparation of this paper; to Dr. C. A. Weatherby for assistance in the nomenclature; and to Mr. C. W. Davison of the Mitchell Park Conservatory of Milwaukee, Wisconsin, for some of the *Pteris cretica* plants used in the investigation.

SUMMARY

The gametophyte of *Pteris cretica* var. *albo-lineata* bears both antheridia and archegonia. The antheridia develop in a normal manner, but all of the archegonia abort.

The nuclei of the gametophyte cells contain 32 chromosomes.

There is no fusion of gametophyte cells and their nuclei before the apogamous embryo begins its development.

The sporophyte is always of apogamous origin and retains the reduced chromosome number.

Eight spore mother cells are produced in each sporangium. There are no meiotic divisions preceding the formation of the spores. The mother cells contain 32 chromosomes, the haploid number. The mother cells appear to pass through synapsis but there is no pairing of chromosomes. Two divisions, which are mitotic in nature, result in the formation of 32 haploid spores.

No fusions of the sporogenous cells and no incomplete nuclear and cell divisions were observed in the spore sacs of *Pteris cretica* var. *albo-lineata.*

Since the nuclei of the sporophyte also contain 32 chromosomes, both the gametophyte and sporophyte possess the haploid number of chromosomes.

Abortion of the sporogenous tissue may occur at any time during the development, starting with the archesporial cell and extending through to the formation of the spores. Abortion of the sporogenous cells results in the disintegration of the nuclear and cytoplasmic material.

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A Brief History of Chinese Herbs and Medicine

Leonard Chan[1]

Modern Western medicine, though still occasionally hampered by tradition and custom, is largely a product of experimental research. Contrasted with this is the Chinese system of medicine which is the product of untold generations of experience and which, despite the invasion of Western ideas and customs into other phases of Chinese life, is extensively practiced today just as it was thousands of years ago. Since several ancient Chinese drugs have been adopted by American and European doctors, and since many Americans, especially in California and other Pacific Coast states, have been helped by Chinese "herb doctors," it seems of interest to briefly investigate the origin of their art.

The science and art of medicine in China go back to such remote antiquity that only legends exist to tell of the first medicinal use of herbs and other products. The study is complicated further because fact and legend are sometimes almost inextricably interwoven.

According to some of the more authentic sources, Shen Nung,[2] who lived about 2700 B.C., discovered that different kinds of vegetables and plants reacted differently in his body, and he is credited with having tested the medicinal action of some 360 varieties of plants on his own system. He found that some of these could be used to cure, or at least to allay the discomfort of certain bodily disorders. He discovered that by mixing different plants in one preparation, it was possible to accentuate or modify certain qualities of the plants. Altogether, he compounded and recorded 113 different prescriptions, some of which are used today.

Legend has it that his system was transparent and that by observing the path that herbs took when he ate them, he was able to tell the specific part of the body to which the particular herb was directed. Thus he could list a specific use for each plant. Because of the transparent system, an abnormal condition following the use of a poisonous drug was readily detected, and before the poisons could affect him he counteracted their action by drinking a concentrated extract of licorice as an antidote. This is still used among the Chinese as an antidote for many poisons.[3]

1 The author accepts full responsibility for the authenticity of the statements in this paper, but appreciatively acknowledges the criticisms of Dr. Robertson Pratt in the preparation of the manuscript.

2 The Chinese characters are translated in Mandarin, the official Chinese dialect.

3 Of course, the author does not recommend this as a generally applicable antidote for poisons. It is merely mentioned as a traditional use among Chinese.

One of the most important laws set down by Shen Nung was the method of compounding prescriptions. He based the method on four characters, "emperor," "premier," "assistant," and "guide," respectively. He believed that when compounding a prescription, the proper kind of herb must be selected to act in the proper capacity according to these four characters: thus, there must be the "emperor" or the main herb which has full control of the disease concerned, the "premier" which advises the main herb as to the way it is to act, the "assistant" which will help the main herb so that it will be able to act better, and the "guide" which will prepare the way for the main herb. The philosophy of Shen Nung still lives, and this method of compounding drugs is universally employed by Chinese herb specialists.

Another important doctrine of the Chinese herbalist is the "pulse law." This too is of ancient origin. After becoming premier in the court of the emperor, Huang Ti, about 2205 B.C., Chi Pai became perturbed over the sickness and suffering of his subjects. In an effort to find means to relieve the suffering and to prevent the spread of disease he held daily conferences with the emperor to discuss methods of accomplishing these ends. The results of these conferences were recorded in nine volumes, known as Ling Shu. It is in these that first mention of the "pulse law" is found.

According to the "pulse law," all sickness may be diagnosed by feeling the pulse. In feeling the pulse, the physician uses three fingers, each of which pertains to a different organ. When feeling the patient's right hand, the speed of the pulse when felt by the second finger pertains to the lung; the third finger to the stomach and the fourth finger to the spleen. When taking the pulse from the patient's left hand, the second finger pertains to the heart, the third finger to the liver, and the fourth finger to the kidney. It is believed that the pulse felt with light pressure of the fingers pertains to the system in general, that felt with moderate pressure pertains to the internal organs, and that felt with heavy pressure pertains to the lower part of the body.

The pulse itself is based on four definitions. If it has a floating effect—i.e. feels like the touch of a piece of wood floating on water, it means that the patient is feverish; if the pulse has the effect of sinking, as if a piece of iron were to sink, it means that there is slow circulation and there is weakness throughout the whole body; if it is slow yet regular, there is merely slow circulation of the blood, and if the pulse is rapid, but regular, the blood is circulating too fast. After the diagnosis, suitable herbs are prescribed to counteract these different conditions.

Chi Pai also wrote nine volumes on the circulation of blood. These books are called Soo Wun and in them it is stated that the origin of all illness is in one or more of five parts of the body, i.e. heart, liver, stomach (including intestines and spleen), lungs and the kidneys. It is believed that since the blood circulates to these different organs, the origin of a disease may be located by merely feeling the pulse relating to the different parts of the body.

In 651 B.C., during the great wars of China, Bien Chok revised the books dealing with herbs. He selected the more useful herbs and discarded the others. His work did much to make the people believe that diseases could be cured, and even prevented, by the use of medicine. He believed that the spread of contagious diseases could be checked and plagues and epidemics prevented by the judicious use of herbs. Since surgery was still an unknown art, and theories of vaccination had not yet been developed, he had ample opportunity for "clinical" testing of his theory of "drinking medicines."

It was not until 190 A.D., during the romance of the Three Kingdoms, that a young physician, Hua To, conceived the ideas that only small quantities of medicine are needed to cure diseases and that many diseases do not originate in internal organs, but are due to external causes. He believed that certain diseases could be cured without the use of medicine. The opportunity to prove his theory came when he was called to treat Kwan Kung, a great warrior who had been struck by a poison dart. Hua To declared that only an operation would prevent death. As Kwan Kung was young, he was willing to try the new method. Of course anaesthetics were unknown, and it is stated that during the operation he diverted his mind from the ordeal by playing chess with his good arm. Thus Hua To became famous as the first surgeon. A few years later, Tsao Tsao, a prince of the Kingdom of Wei, was suffering from an infection of the brain. The most famous doctors of his country were unable to cure him, and so he sent to the Kingdom of Han for Hua To. After diagnosing the case, Hua To stated that only an operation would save the prince, whereupon Tsao Tsao became suspicious. Since he belonged to a rival kingdom, the prince thought himself the victim of a conspiracy and so he ordered the execution of Hua To. China lost her first and most famous surgeon.

Before departing from his homeland Hua To left, with his wife, written records of all his operations. After the execution, his wife, thinking the papers worthless, took them out of the house and burned them. A few papers which were not burned were later found by a passerby who, realizing their value, preserved them. It happened that these last few pages

described the castration of pigs and hens in order to fatten them before slaughter. This same method is used in China today, so his art was not lost forever.

During the Han Dynasty (206 B.C.—220 A.D.) schools were established where the use of Chinese herbs was taught. Chang Chung-ching was among the first to write text-books and he based his teachings on the works of Bien Chok. He included the 113 prescriptions of Shen Nung and compounded many new ones. Among them was the famous cinnamon Twigs Tea, which forms the basis of many herb teas used today.

The Chinese believe that poisonous substances may leave the body when the pores of the skin are opened. Thus, this tea which generally induces sweating, is used extensively. It is brewed from a mixture of cinnamon twigs; pai chao; glycyrrhiza, previously boiled with honey to bring out its flavor; ginger; and dates. When drinking the tea does not produce sweating, Ma Huang, the source of ephedrine, is added. Thus it may be seen that this tea is based on the theory of Shen Nung. Cinnamon twigs act as the "emperor" since they increase the circulation of the blood and are stimulant, thus inducing perspiration; pai chao is the "premier" and acts as an antipyretic, counteracting high temperature and presumably aiding thereby the departure of poisonous substances. Ginger is a carminative and acts as the "assistant." Dates and glycyrrhiza act as "guides," the former being a stimulant to the intestinal tract and the latter a vehicle and flavor. It should be noted that this prescription is in harmony with the belief that all sicknesses originate in the heart, lungs, liver, stomach or kidneys. Thus, the ingredients of this tea supposedly influence the heart, stomach, and liver. Ma Huang is added for its effect on lungs and bronchial system.

During the Tang Dynasty (617 A.D.-906 A.D.) many of the old prescriptions were revised and remarkable progress was made in the treatment of malaria and other fevers.

The Sung Dynasty (959 A.D.-1278 A.D.) made little, if any progress in the art of healing.

In the kingdom of Gin about 1100 A.D., however, there were two famous physicians. Li Tung-yuan specialized in disorders of the spleen and the stomach because he said that all things when taken internally must pass through the stomach and then be filtered through the spleen before going to the peripheral system. The other physician, Liu Ho-chien, opposed this theory and claimed that diseases are caused by living organisms found in the soil, and that because food is grown in soil it becomes infested with these organisms. He believed that if all food were sterilized there

would be no disease or sickness. These two physicians finally reconciled their ideas and proposed a theory of disease that became famous during their time.

Both the theories and practice of medicine seemed to take a step backward during the Yuan Dynasty (1278 A.D.-1368 A.D.). Chu Tan-kai formulated the theory of Ying and Yang, i.e. all sicknesses were believed to be either positive or negative. According to this theory, Summer diseases were positive, Winter diseases were negative and Spring and Autumn diseases were combinations of the two. It was believed that negative medicine must be used for a positive disease and vice versa. Chang Tze-ho, on the other hand, claimed that evil spirits were the cause of sicknesses and relied on prayers, incantations, and charms for their cure.

It was not until the Ming Dynasty (1368 A.D.-1643 A.D.) that medicine began to progress rapidly. Four famous professors taught in the National University during this period. Shi Lih-tsai, whose books are still used by beginners, specialized in compounding new herb formulas. Li Shi-stai stated that we really do not need herbs or drugs, because if we were to eat the right kinds of foods we would never be sick. Thus the herbs are really tonics. Chang Ching-ngoh specialized in epidemic diseases, and Li Shih-tsen divided diseases into two opposing forces. He declared that in treating a disease an herb should be used that would produce an effect opposite to that of the sickness. He discovered and used many new medicines, not only herbs from the vegetable kingdom, but also many preparations from the animal kingdom.

The last period of great discoveries of Chinese herbs was the Ching Dynasty (1644 A.D.-1911 A.D.). This dynasty contributed two great physicians. One of them, Yieh Tien-Shih, known as the "wizard physician," gained a reputation as being one who could cure any kind of ailment. According to legend, one day he passed a funeral procession, and by inquiry learned that the deceased was a pregnant woman who had suffered a strange death. Upon being granted permission to look at her, he declared that woman was not dead, but that the heart had appeared to stop because the child had seized it. With permission he stabbed a silver needle into the chest. The needle pricked the hand of the child who released its hold on the heart. The woman lived and the child was born.

The other, Chen Shiu-yuan, investigated the nine volumes of Ling Shu and selected five important prescriptions with which he effected many remarkable cures. Pan Hsia Tea was used to cure coughs caused by fevers; chi-shi-li-fang, consisting of egg whites mixed with wine, was used to cure disorders of the stomach; wu-chia-yu-ku, the pulverized powder of

"octopus bones," was used as a blood tonic and to disintegrate blood clots; and Tieh-lo was used to cure cerebral disorders and also as a blood tonic. This consisted principally of iron rust and was used because it was thought that the iron would cause the organisms to adhere to it and being heavy would sink, thereby preventing the organisms from entering the head. The fifth and last was chieh-sieh-pai-shu which supposedly caused the disappearance of phlegm in the throat and strengthened the spleen.

Since 1911 Western medicine has permeated China and now modern, scientific methods are used extensively. A National Institute of Chinese Herbs has been established for the scientific study and analysis of old Chinese remedies. Progress has been slow, but some of the results are encouraging. Many of the old remedies contain very active constituents, and it seems reasonable to believe that although the philosophy and theory of compounding Chinese prescriptions may seem strange to the Western mind, some of the Chinese preparations may prove to be of inestimable value to American and European physicians. Ephedrine has already been isolated from Ma Huang. What will be next?

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Thiamin and Symbiosis

William J. Robbins

(with one figure)

Schopfer (6, 7) and others (3, 5) have demonstrated that *Phycomyces Blakesleeanus* requires thiamin (vitamin B_1) and is unable to synthesize this growth substance from sugar, asparagine and minerals. When an agar medium lacking thiamin is inoculated with spores of *Phycomyces* the growth is extremely sparse. Although the hyphae range widely in or on the surface of the agar the individual hyphae are widely separated, no surface mat of mycelium is formed, no sporangiophores are produced and the total growth is limited to a dry weight of a milligram or less. The addition of thiamin to such a medium permits a luxuriant development; the agar becomes covered with a mycelial mat and sporangiophores are produced freely.

Some other fungi resemble *Phycomyces* in their inability to synthesize thiamin but there are many which are autotrophic for this growth substance (3). They synthesize it from elementary constituents and grow in a medium which lacks thiamin. Many of the common saprophytes, as well as some parasites, belong in this group. In fact, thiamin appears necessary for the existence of all or almost all organisms, both plant and animal, and those unable to synthesize it must secure their supply of this essential substance from that made by other organisms.[1] In other words, one part of the living world depends for thiamin upon another in somewhat the same fashion as one part depends upon the other for carbohydrates or for organic nitrogen.

The dependence of an organism heterotrophic for thiamin upon one autotrophic for the same substance is illustrated in Figure 1. In this instance a medium was prepared containing per liter 100.0 g dextrose, 1.0 g asparagine, 0.5 g $MgSO_4 \cdot 7\,H_2O$, 1.5 g $KH_2\,PO_4$ and 10 g bacto-agar. To each liter 0.1 ml of the following mineral supplements was added: 5.7 mg H_3BO_3, 18.6 mg $CuSO_4 \cdot 5\,H_2O$, 173 mg $FeNH_4\,(SO_4)_2 \cdot 18\,H_2O$, 8.1 mg $MnSO_4$, 4 H_2O, 3.6 mg ammonium molybdate 85 per cent, 79 mg $ZnSO_4$, 7 H_2O, distilled water 100 ml. Approximately 25 ml of this medium was poured in petri dishes and inoculated with a spore suspension of *Phycomyces*, plus strain. A scanty vegetative growth characteristic of that on a medium lacking thiamin developed. However, a colony of *Penicillium sp.* appeared as a contaminant in some of the plates. In spite

[1] This statement is not entirely correct since the successful synthesis of thiamin in vitro makes a supply available which may be used to supplement that made in vivo.

of the deficiency of thiamin this organism grew well, evidently synthesizing the necessary growth substance; its heavy mycelial mat, fruiting freely, covered a portion of the plate and overgrew the hyphae of *Phycomyces* in that portion of the agar. In two or three days *Phycomyces* sporangiophores, several centimeters long, grew up through the mat of the contaminant; but they appeared nowhere else on the plate. In the photographs in figure 1 the faint outline of the scanty growth of *Phycomyces* in the major portion of the petri dish, the heavy growth of the contaminating fungus and the sporangiophores of *Phycomyces* extending out through the

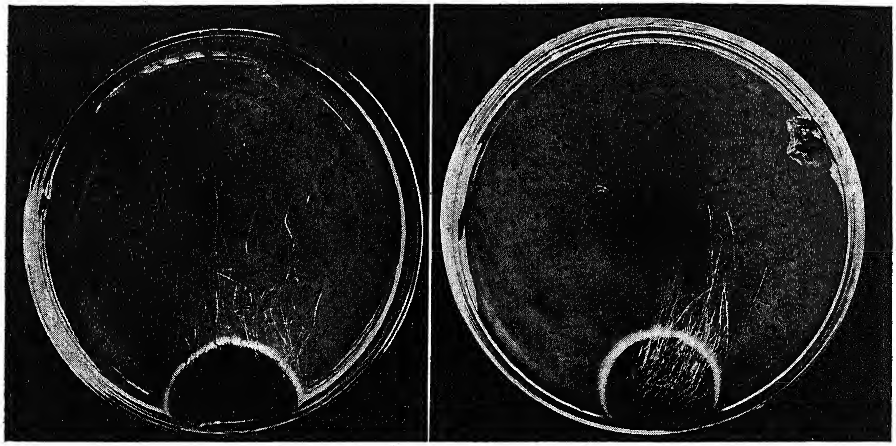

Fig. 1. Growth of *Phycomyces* on agar containing sugar, asparagine, mineral salts but no thiamin. Note scanty growth with absence of sporangiophores in major portion of plates, heavy growth of contaminating *Penicillium* and normal sporangiophores of *Phycomyces* springing from the contaminating colony. The growth on the right-hand plate is the younger.

mat of the contaminant are shown. It appears clear that the thiamin so necessary for the development of *Phycomyces* was supplied by the *Penicillium*.

It is of some interest to speculate on how the thiamin made by the *Penicillium* reached the hyphae of the *Phycomyces*. Did it diffuse from the living hyphae into the agar or did the older hyphae age, autolize and set the thiamin free? We are inclined to believe that the latter explanation is the more probable since the beneficial effect of the *Penicillium* did not extend beyond the limits of the colony as we should expect if the thiamin diffused from the normal living cells. In any event it seems clear that the *Penicillium* made more thiamin than was required for its growth and some of the excess became available for *Phycomyces*.

Others (2, 4, 8, 9, 10) have called attention to a similar relation between microorganisms autotrophic for thiamin and those heterotrophic for the same substance and have pointed out the significance of such observations for an explanation of the nutritional relations which may exist in some instances of symbiosis and parasitisin. The relation between the *Penicillium* and *Phycomyces* in this instance is not strictly symbiosis since only one organism (the *Phycomyces*) benefited; nevertheless, such observations suggest possible nutritional relationships between symbionts and between parasite and host other than those involving carbohydrate and nitrogen compounds hitherto commonly assumed.

While the growth substance involved in the example described in this paper is thiamin it should be emphasized that other growth substances may be concerned in the relationship between organisms. Kögl and Fries (1) have described instances in which one fungus supplies biotin and another thiamin, each supplementing the other's deficiencies. We will doubtless in time discover many other examples in some of which deficiencies of more than one growth substance may be supplied by the synthetic activity of organisms completely autotrophic for growth substances.

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Studies of Mexican and Central American Plants—VIII[1]

C. L. LUNDELL

(WITH FOUR FIGURES)

In studies of the Polygonaceae of the Yucatan Peninsula, preparatory to publication of an account of the polygonaceous flora of that region, a review of the Mexican and northern Central American species of *Coccoloba* has been undertaken. It is evident that Lindau's monograph (Bot. Jahrb. Engler **13**: 106–229. 1890) is very outdated, and that a complete revision of the genus would be desirable to take into account the numerous species described since his treatise appeared. Interpretation of the species is often difficult for many of them are dioecious, a fact evidently overlooked by most past workers presumably because of the paucity of complete material. Staminate flowers usually are pseudohermaphroditic. Since publication of a general account of the genus will be delayed, six species from the Yucatan Peninsula are now proposed as new.

The other novelties in this paper are based primarily on material obtained by Mrs. Lundell and the writer in Yucatan and Quintana Roo, Mexico, during the summer of 1938,[2] recent collections of Mr. Percy H. Gentle in British Honduras, and collections of Mr. Eizi Matuda on Mt. Tacana, Chiapas during March and April, 1939.

In the study, types and other specimens have been borrowed from the Field Museum (F), Gray Herbarium (G), New York Botanical Garden (NY), and the Yale School of Forestry (Y); grateful acknowledgment is made to the directors and curators for this courtesy. A majority of the

[1] Papers from the Herbarium of the University of Michigan. Previous issues in this series have appeared as follows: I, Carnegie Inst. Washington Publ. 478: 208–221. 1937; II, Phytologia **1**: 212–222. 1937; III, ibid. **1**: 241–247. 1937; IV, Field and Laboratory **6**: 9–16. 1937; V, Amer. Midland Nat. **19**: 427–432. 1938; VI, ibid. **20**: 236–242. 1938; and VII, Lloydia **2**: 73–108. 1939.

[2] Lundell, C. L. The 1938 botanical expedition to Yucatan and Quintana Roo, Mexico. Carnegie Inst. Washington Year Book No. 37: 143–147. 1938.

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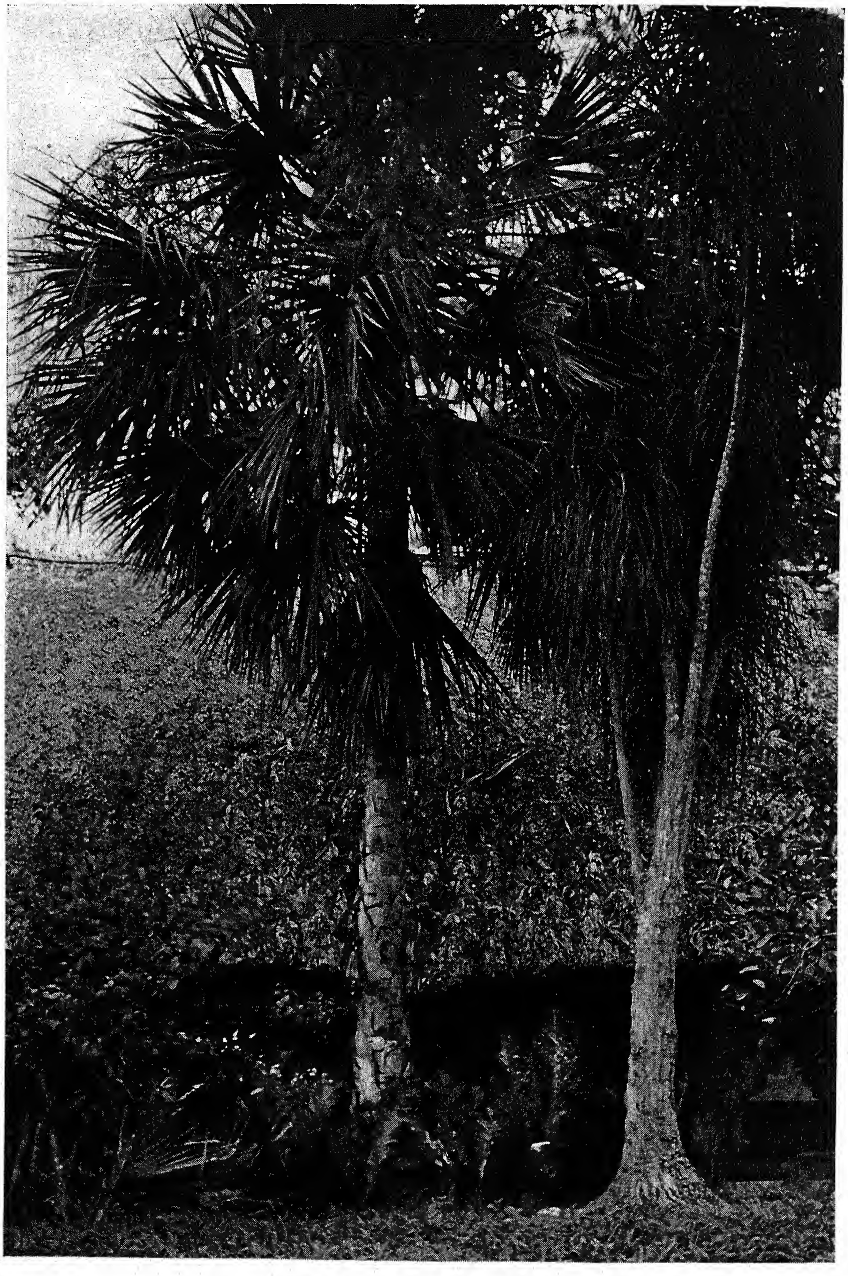

Fig. 1. *Beaucarnea Ameliae* Lundell. Note the slender erect branches and comparatively small bulbous base of trunk. The palm is a native species of *Sabal*.

cited specimens are in the University of Michigan Herbarium (M). To the Carnegie Institution of Washington and the Horace H. Rackham School of Graduate Studies of the University of Michigan the writer expresses his thanks for financial support of both field and herbarium studies.

Beaucarnea Ameliae sp. nov. (fig. 1).—Arbor 4–8 m. alta, basi expansa, caule 20–25 cm. diam. Folia ramorum apice congesta, linearia, basi amplexicaulia, 2.5–4.8 cm. lata, supra basin constricta, 1–1.5 cm. lata, sursum usque ad 3 cm. lata, apice setiformia, 85–105 cm. longa, minutissime serrulata. Inflorescentiae ♂ paniculatae, pyramidales, usque ad 75 cm. altae; pedicellis 5–7 mm. longis; segmentis perianthii ellipticis, 4 mm. longis, 3 mm. latis. Filamenta ca. 2 mm. longa. Antherae ca. 2.2 mm. longae. Segmenta perianthii ♀ 3–3.3 mm. longa, 1.8–2 mm. lata. Ovarium trialatum. Pedicelli fructiferi 5–9 mm. longi. Fructus 3–alatus, late ellipticus vel obovato-ellipticus, 13–18 mm. longus.

A tree 4 to 8 m. high with a thickened bulbous base contracted into a stem 20 to 25 cm. in diam. Branches erect, rather slender. Leaves clustered at apex of branches, crowded, linear, flat, the base amplexicaul, 2.5 to 4.8 cm. wide, the constriction immediately above base short, 1 to 1.5 cm. wide, the blade up to 3 cm. wide about 30 cm. above base, tapering to a long setiform tip, usually 85 to 105 cm. long, sometimes shorter, the margin microscopically serrulate with uniform appressed teeth, the grooves smooth and punctate. Staminate inflorescence (*Lundell and Lundell 8128*) entirely glabrous, openly paniculate, pyramidal, up to 75 cm. high, the lower primary branches subtended by leafy bracts up to 58 cm. long, the bracts subtending upper branches much reduced, the primary branches up to 32 cm. long; flowers in fascicles of 2 or 3, pale yellow, nearly white, subtended by thin ovate-lanceolate bracteoles 6 to 7 mm. long; pedicels jointed at or slightly below middle, 5 to 7 mm. long; perianth segments thin, elliptic, 4 mm. long, 3 mm. wide, slightly erose, reflexed at anthesis; stamens 6, opposite the perianth segments; filaments about 2 mm. long; anthers versatile, about 2.2 mm. long; ovary rudimentary. Pistillate inflorescence (*Gaumer 24327*) similar to staminate; pedicels 4 to 5 mm. long; perianth segments elliptic, entire, 3 to 3.3 mm. long, 1.8 to 2 mm. wide; stamens rudimentary, the anthers less than 1 mm. long; ovary 3–celled, 3–winged, with two erect ovules in each cell; style 3–winged; stigma thick, 3–lobed. Fruiting pedicels 5 to 9 mm. long. Fruits 1–celled, 1–seeded, 3–winged, broadly elliptic or obovate-elliptic, 13 to 18 mm. long, wings longer at apex than base, apex with an open sinus, base emarginate. Seeds shallowly 3–lobed, inaequilateral, globose, 3.5 to 4 mm. long.

Type in the Herbarium of the University of Michigan, *C. L. Lundell and Amelia A. Lundell 8128*, staminate flowers, collected in denuded lime-

stone flats bordering *cienaga*, km. 29, Merida-Progreso road, Yucatan, Mexico, July 26, 1938.

ADDITIONAL SPECIMENS EXAMINED: MEXICO: Yucatan, Kancabtsonot, Jan., 1917, *G. F. Gaumer 23520* (F); without locality, 1917-1921, *Gaumer 24327* (F); Chichen Itza, in old clearing, June 23, 1932, *W. C. Steere 1498* (M); Noh Itza, km. 104 on Merida-Chichen Itza road, a grove in advanced deciduous forest, June 15, 1938, *Lundell and Lundell 7566* (M). Quintana Roo, Coba, in fire-swept deciduous forest east of ruins, July 2, 1938, *Lundell and Lundell 7763* (M). BRITISH HONDURAS: El Cayo District, Mountain Pine Ridge, San Agustin, on crest of limestone hill bordering pineland, July 28, 1936, *Lundell 6650* (M).

DISTRIBUTION: Yucatan, Quintana Roo, and central British Honduras. It is fairly common in the xerophytic cactus area along the northwest coast of Yucatan, but only two groves were found inland, one at Noh Itza not far from Chichen Itza, and the other east of Coba in Quintana Roo. A single tree was encountered on a limestone hill at San Agustin, British Honduras, but a grove of the species was observed on a hillside near Rio Privacion, bordering the Mountain Pine Ridge.

VERNACULAR NAMES: "tsipil" (*Gaumer 23520; Lundell and Lundell 7566*); "chit" (*Steere 1498*).

B. Ameliae and *B. petenensis* (Lund.) Lund. resemble *B. guatemalensis* Rose. The latter has a finely scabrous leaf surface, a well marked characteristic apparently not observed by Rose (Contr. U. S. Nat. Herb. **10**: 88. 1906). The two peninsula species have entirely smooth blades. *B. petenensis* is known only from sterile material, but appears amply distinct from *B. Ameliae* in its leaves which are 115 to 140 cm. long compared with 85 to 105 cm. long in the latter. The narrow prolonged constriction above the base of the leaf and a maximum blade width of only 2 cm. distinguish it further.

Beaucarnea petenensis (Lundell) comb. nov. *Dracaena petenensis* Lundell, Journ. Wash. Acad. Sci. **25**: 230. 1935.—A tree 6 to 12 m. high with a thick bulbous base 70 to 90 cm. in diam.; trunk 20 to 30 cm. in diam. Branchlets 10 to 15 mm. in diam. 15 cm. below apex. Leaves numerous, crowded at apex of branchlets, pendent, linear, flat, the base amplexicaul, up to 3.5 cm. wide, the constriction immediately above base elongate, about 7 mm. wide, the blade up to 2 cm. wide 30 cm. above base, tapering to a long setiform tip, usually 115 to 140 cm. long, the margin microscopically serrulate with uniform subappressed teeth, the grooves smooth. Flowers and fruits unknown.

Specimen examined: GUATEMALA: Department of Petén, Monte Hiltun, a grove in limestone valley forest, May 17, 1933, *Lundell 3271*, type (M).

No fertile material of this species has been collected, but its habit and leaf characteristics are those of a *Beaucarnea.*

Nolina pliabilis (Baker) comb. nov. *Dasylirion pliabile* Baker, Journ. Linn. Soc. Bot. **18**: 240. 1880. *Beaucarnea pliabilis* (Baker) Rose, Contr. U. S. Nat. Herb. **10**: 89. 1906.—Reported to be a tree. Leaves rather thick, rigid, linear, concave, the base amplexicaul, about 17 mm. wide, constricted above into a narrow blade 3 to 4 mm. wide, possibly 60 cm. long, the margin armed with irregularly spaced incurved prickles visible to the naked eye, the grooves very narrow, microscopically papillate. Pistillate flowers usually geminate with an undeveloped third bud, subtended by thin, keeled, ovate, erose bracteoles 2 to 2.5 mm. long; pedicels jointed above the middle, about 2.5 mm. long, accrescent rapidly after anthesis becoming 4 to 5 mm. long with joint below middle; perianth segments entire, thin, ovate-oblong or oblong-elliptic, 2 to 2.1 mm. long, 1 to 1.2 mm. wide, apex papillate; stamens rudimentary, much shorter than perianth segments; ovary 3-celled, 3-lobed with 2 ovules in each cell; stigma subsessile, small, 3-lobed. Immature fruits deeply 3-lobed, the lobes rounded, divaricate, usually with 1 ovule developing in each cell.

Specimen examined: MEXICO: Yucatan, in littoral area near Sisal, Oct. 24, 1865, *Arthur Schott 892*, type collection (F).

Vernacular name "tzipil."

Baker (l. c.) described the species as having leaves up to 15 mm. wide and 60 cm. long, with fruiting pedicels about 3 mm. long, and fruits broadly elliptic, about 13 mm. long, 8.5 to 9.5 mm. wide. The Schott specimen in the Field Museum Herbarium bears a single broken leaf 4 mm. wide, and has pedicels up to 5 mm. long. I have not seen the type specimen which is in the British Museum Herbarium; my interpretation of the species is based on the cited isotype.

Rose (l.c.) evidently did not see type material of *N. pliabilis*, and confused the species with *Beaucarnea Ameliae* Lundell. The leaves, flowers and fruits of *Schott 892* (F) are typical of the genus *Nolina.*

Coccoloba corozalensis sp. nov. (fig. 2).—Arbor, 10–15 cm. diam. Ramuli glabri. Folia petiolata, petiolo 5–11 mm. longo, glabra, chartacea vel subcoriacea, ovato-elliptica, late elliptica vel obovata, 5–12 cm. longa, 2.5–7.3 cm. lata, apice rotundata vel raro late obtusa, basi rotundata, raro subcuneata, minute reticulato-venosa. Inflorescentiae terminales, spicatae vel subspicatae, 7–14 cm. longae, pedunculis 2 cm. longis vel minoribus, rachidibus glabris,

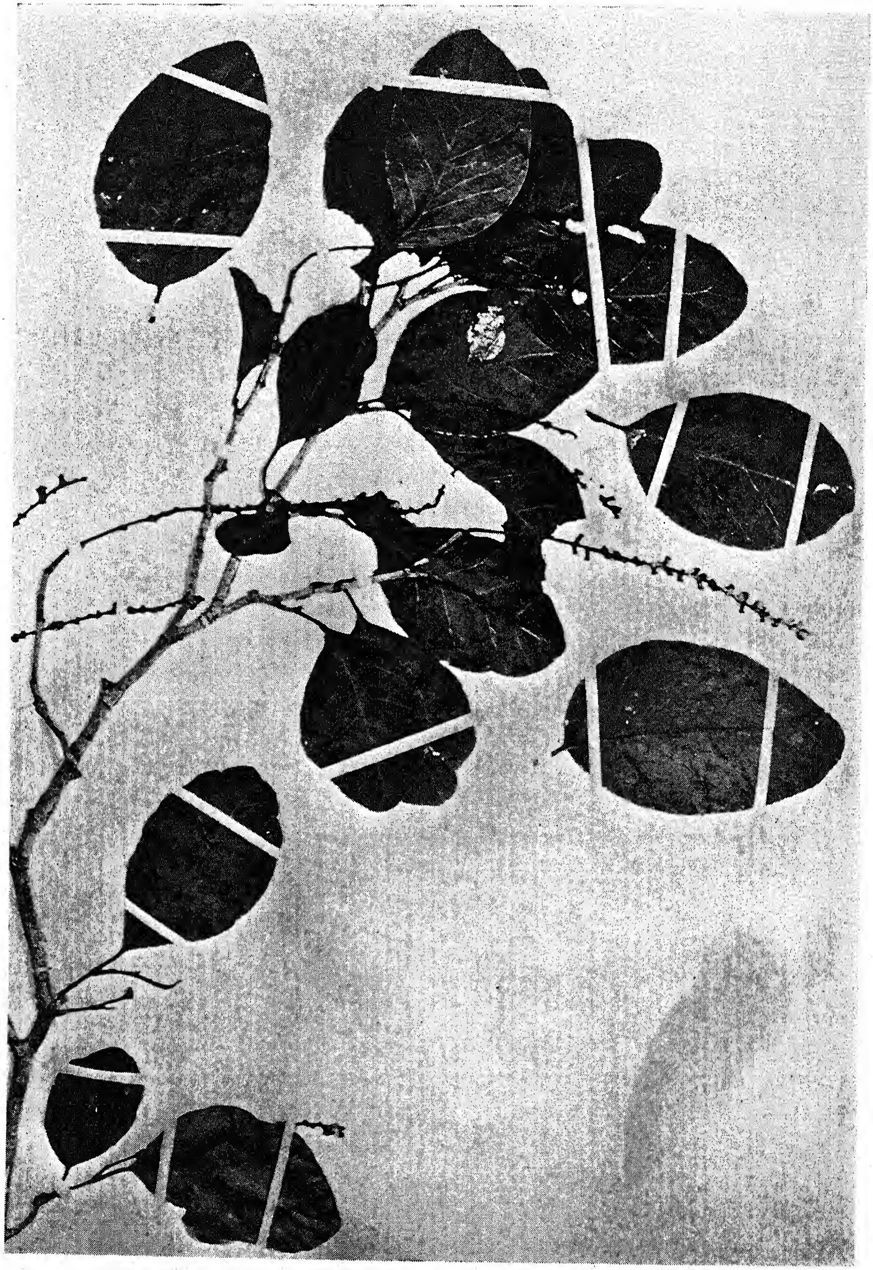

Fig. 2. *Coccoloba corozalensis* Lundell. Type (*Lundell 4908*), in Herbarium of the University of Michigan. $\times \frac{1}{2}$.

nodulis 1–floris, raro 3–floris; bracteae ca. 1 mm. longae; ochreolae bracteam superantes. Flores dioici, subsessiles. Perianthii ♀ tubus cylindricus, 1 mm. longus, lobis oblongo-ellipticis vel ovato-ellipticis, rotundatis, 1–1.4 mm. longis. Stamina abortiva. Ovarium 1.2–1.5 mm. longum. Styli 3, exserti. Pedicelli fructiferi ochreolis breviores. Fructus ovoideus, 7–9 mm. longus, 5–6 mm. diam., basi rotundatus, apice obtuse acuminatus.

A tree 10 to 15 cm. in diam.; branchlets glabrous, rather short and slender. Stipules 5 to 9 mm. long, glabrous, thin, the tube tightly sheathing stem, petiole basal. Leaf blades entirely glabrous, chartaceous at first, subcoriaceous with age, ovate-elliptic, broadly elliptic or obovate, 5 to 12 cm. long, 2.5 to 7.3 cm. wide, apex rounded or rarely bluntly obtuse, base usually rounded, sometimes decurrent and subcuneate, costa prominent beneath, nearly plane above, main lateral veins 5 to 8 on each side, veinlets finely and closely reticulate, veins and veinlets prominulous on both surfaces. Petioles sulcate, glabrous, 5 to 11 mm. long. Inflorescence terminal, spicate or subspicate, 7 to 14 cm. long, few flowered, glabrous; peduncles up to 2 cm. long; rachis slender; nodules usually 1–flowered, sometimes 3–flowered (*Kluge 17*); bracts broad, rounded, about 1 mm. long; ochreolae slightly exceeding bracts, thin, truncate, bracts and ochreolae bearing within a few short red hairs. Flowers dioecious, subsessile at anthesis, the pedicels accrescent. Pistillate flowers: perianth tube cylindrical, 1 mm. long, thick; lobes oblong-elliptic or ovate-elliptic, rounded, 1 to 1.4 mm. long. Stamens rudimentary, 0.5 mm. long or less. Ovary slender, 1.2 to 1.5 mm. long; styles 3, 1 to 1.2 mm. long; stigmas exserted. Fruiting pedicels shorter than ochreolae. Fruits purple-black when ripe (*Bartlett 11281*), ovoid, 7 to 9 mm. long, 5 to 6 mm. in diam., base rounded, apex obtusely acuminate, the acumen formed by the persistent perianth lobes.

Type in the Herbarium of the University of Michigan, *C. L. Lundell 4908*, collected in *acahual*, Xiabe, Corozal District, British Honduras, Aug. 21, 1933.

Additional specimens examined: BRITISH HONDURAS: Corozal District, Xiabe, Aug. 21, 1933, *Lundell 4908*, type collection (F-2). Orange Walk District, Honey Camp, Sept., 1929, *Lundell 347* (F). Belize District, Maskall, in hammock in pineland, Jan. 31, 1934, *Percy H. Gentle 1113* (F, M). Cornhouse Creek, in thicket above mangrove between river and pine ridge, Jan. 31, 1931, *H. H. Bartlett 11281* (M). Without locality, *Kluge 17* (Y).

Distribution: Coastal areas of northern and central British Honduras.

Vernacular names: "uva cimarron" (*Lundell 4908*); "pigeon plum" (*Gentle 1113*); "wild grape" (*Kluge 17*).

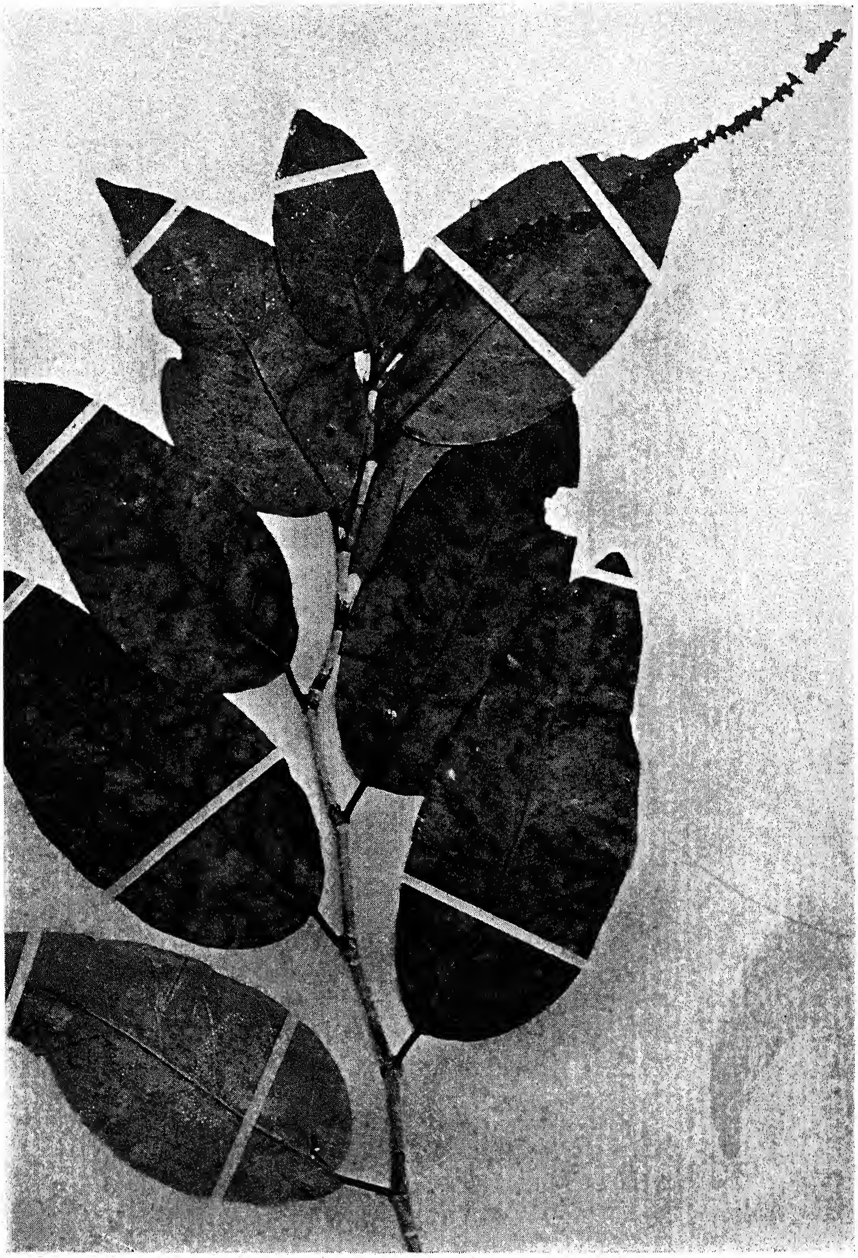

Fig. 3. *Coccoloba Gentlei* Lundell. Type (*Gentle 56*), in Herbarium of the University of Michigan. $\times \frac{1}{2}$.

Coccoloba Gentlei sp. nov. (fig. 3).—Arbor parva. Ramuli glabri. Folia petiolata, petiolo 9–12 mm. longo, glabra, subcoriacea, lanceolata vel lanceolato-elliptica, 7–13.5 cm. longa, 3.5–6.2 cm. lata, apice attenuata, late obtusa vel rotundata, basi rotundata, reticulato-venosa. Inflorescentiae terminales, subpaniculatae, 12–16 cm. longae; spicae compositae, rachidibus glabris, nodulis 1–4–floris; bracteae 1–1.4 mm. longae, glabrae; ochreolae bracteam superantes, glabrae. Flores subsessiles vel breviter pedicellati. Perianthii tubus ca. 1 mm. longus, lobis oblongo-ellipticis, 1.8–2 mm. longis. Ovarium 1–1.2 mm. longum, ut videtur abortivum. Styli 3.

A small tree; branchlets glabrous, striate. Stipules 12 to 13 mm. long, thin, glabrous, the tube tightly sheathing stem, petiole basal. Leaf blades subcoriaceous, entirely glabrous, lanceolate or lanceolate-elliptic, 7 to 13.5 cm. long, 3.5 to 6.2 cm. wide, apex attenuate, bluntly obtuse or rounded, base rounded, costa prominent beneath, nearly plane above, main lateral veins 8 to 11 on each side, rather prominent beneath, less conspicuous above, finely and closely reticulate-veined on both surfaces. Petioles thick, sulcate above, glabrous, 9 to 12 mm. long. Inflorescence terminal, subpaniculate, the central spike 12 to 16 cm. long, bearing 1 or 2 short lateral spikes near base, exceeding leaves; rachis slender, glabrous; nodules 1– to 4–flowered; bracts broad, rounded, 1 to 1.4 mm. long, glabrous; ochreolae exceeding bracts, up to 2 mm. long, truncate, glabrous. Flowers subsessile or with pedicels up to 1 mm. long, shorter than ochreolae. Perianth glabrous, tube about 1 mm. long; lobes oblong-elliptic, 1.8 to 2 mm. long, rounded. Filaments subequaling lobes. Ovary obscurely trigonal, slender, 1 to 1.2 mm. long (abortive?); styles 3. Fruits not known.

Type in the Herbarium of the University of Michigan, *Percy H. Gentle 56*, collected along Belize-Sibun River road, Belize District, British Honduras, 1931–1932. Duplicate in Field Museum Herbarium.

The species is related to *C. corozalensis* Lundell.

Coccoloba hondurensis sp. nov.—Arbor, 13 m. alta. Ramuli glabri, striati. Folia petiolata, petiolo 1–3.5 cm. longo, glabra, subcoriacea vel coriacea, oblongo-elliptica, ovato-oblonga vel obovato-elliptica, 8.5–29 cm. longa, 4–16 cm. lata, apice obtuse apiculata, obtusa, vel abrupte subacuminata, acumine obtusa vel raro acuta, basi obtuso-rotundata, rotundata vel emarginata, reticulato-venosa. Inflorescentiae terminales, simplices vel subpaniculatae, racemosae, 15–45 cm. longae, rachidibus puberulis, nodulis 1–3–floris; bracteae ovato-triangulares, ca. 0.8 mm. longae, puberulae; ochreolae bracteam subaequantes, puberulae. Flores albi, subsessiles; pedicelli fructiferi ca. 2 mm. longi. Perianthii tubus 0.9–1 mm. longus, lobis suborbicularibus vel late ovato-oblongis, 1–1.4 mm. longis. Filamenta 1.4–2.5 mm. longa. Ovarium trigonum, ca. 1 mm.

longum. Styli 3. Fructus subglobosus vel ellipsoideus, 7–12 mm. longus, 7–8 mm. diam., apice basique obtusus vel rotundatus.

A tree up to 13 m. high; branchlets glabrous, striate. Stipules sheathing, ample, up to 13 mm. long, at first puberulent and barbate, glabrescent very early, petiole basal. Leaf blades entirely glabrous, subcoriaceous or coriaceous, oblong-elliptic, ovate-oblong or obovate-elliptic, 8.5 to 29 cm. long, 4 to 16 cm. wide, apex obtusely apiculate, obtuse or abruptly subacuminate, the acumen usually obtuse, sometimes acute, base obtuse-rounded, rounded or emarginate, often inaequilateral, costa prominent beneath, nearly plane at base above, main lateral veins 6 to 10 on each side, prominent beneath, less conspicuous above, finely reticulate-veined on both surfaces. Petioles thick, glabrous, 1 to 3.5 cm. long. Inflorescence terminal, simple or subpaniculate, racemose, 15 to 45 cm. long; rachis minutely and densely puberulent; nodules 1– to 3–flowered; bracts ovate-triangular, about 0.8 mm. long in flower, up to 1.4 mm. long in fruit (*Chickering 233*), obtusish to acute, puberulent; ochreolae subequaling to slightly exceeding bracts in length, puberulent. Flowers white (Bartlett), subsessile, the pedicels lengthening after anthesis, up to 2 mm. long in fruit. Perianth finely lepidote, the tube 0.9 to 1 mm. long; lobes suborbicular or broadly ovate-oblong, 1 to 1.4 mm. long. Filaments 1.4 to 2.5 mm. long. Ovary trigonal, about 1 mm. long; styles 3. Fruits dull pale purple, subglobose or ellipsoid, 7 to 12 mm. long, 7 to 8 mm. in diam., apex and base obtuse or rounded.

Type in the Herbarium of the University of Michigan, *C. L. Lundell 3996*, collected on river bank at Little Cocquericot, Belize River, El Cayo District, British Honduras, June 12, 1933.

ADDITIONAL SPECIMENS EXAMINED: BRITISH HONDURAS: El Cayo District, Little Cocquericot, Belize River, April 30, 1933, *Lundell 3995* (F, M); May 25, 1933, *Lundell 3997* (F, M). Belize District, Manatee Lagoon, Dec. 30, 1905, *M. E. Peck 255* (G). Cornhouse Creek, Manatee River, Jan. 31, 1931, *H. H. Bartlett 11275* (F, M). Sibun River, Feb. 4, 1931, *Bartlett 11361* (M). Tiger Point, Northern River, *Percy H. Gentle 897* (F, NY, M). Stann Creek District, Silk Grass Creek Reserve, Jan. 1, 1926, *S. J. Record* (*B. H. 20, Yale 8788*) (Y). Middlesex, along river bank, Nov. 15, 1929, *W. A. Schipp 453* (F, M, NY). GUATEMALA: Department of Izabal, vicinity of Quirigua, alt. 75–225 m., May 15–31, 1922, *P. C. Standley 23988, 24547, 24601* (NY). HONDURAS: Department of Santa Barbara, San Pedro Sula, March, 1889, *C. Thieme* (*Donn. Smith 5433*) (F). Department of Atlantida, vicinity of Tela, at sea level, 1927–1928, *P. C. Standley 53716, 54476, 54481, 54752, 56598, 56659* (F). East of Tela, near lagoon, June-July, 1929, *A. M. Chickering 233* (F, M).

Distribution: Wet lowlands of central and southern British Honduras, eastern Guatemala, and northern Honduras. It has been found chiefly on river banks and in wooded swamps of the coastal areas.

Vernacular names: "uva" (*Standley 53716*); "cordoncillo" (*Standley 24601*); "wild grape" (*Record B. H. 20*).

The specimens show considerable variation, especially in leaf shape, inflorescence, and fruits, but all appear to be referable to a single species. The flowers are dioecious, but the pistillate ones available are not in satisfactory condition for description. Collections of *C. hondurensis* have been referred to *C. Schiedeana* Lindau, *C. marginata* Benth., *C. barbadensis* Jacq., and *C. leptostachya* Benth. I have not been able to associate the species with any of these.

Coccoloba lancifolia sp. nov.—Arbor, 8 m. alta, 12.5 cm. diam. Ramuli glabri. Folia petiolata, petiolo 5–10 mm. longo, glabra, chartacea vel subcoriacea, lanceolata vel lanceolato-oblonga, 4.5–7.5 cm. longa, 1.8–3.3 cm. lata, apice attenuata, obtusa vel obtuse acuminata, basi rotundata, reticulato-venosa. Infructescentiae terminales, racemosae, rachidibus glabris, nodulis 1–3–floris; bracteae et ochreolae minutae, glabrae. Pedicelli fructiferi crassi, 2.5–3.5 mm. longi. Fructus ovoideus, 11–12 mm. longus, 7–9 mm. diam., apice obtuse apiculatus.

A tree, 12.5 cm. in diam., 8 m. high; branchlets glabrous, short. Stipules closely sheathing, 3 to 6 mm. long, petiole basal. Leaf blades entirely glabrous, chartaceous or subcoriaceous, lanceolate or lanceolate-oblong, 4.5 to 7.5 cm. long, 1.8 to 3.3 cm. wide, apex attenuate, obtuse or obtusely acuminate, base rounded, slightly emarginate or decurrent, inconspicuously inaequilateral, costa prominent beneath, plane above at base, main lateral veins 4 to 6 on each side, reticulate-veined, veins and veinlets prominulous on both surfaces. Petioles slender, sulcate above, 5 to 10 mm. long, glabrous. Infructescence terminal, racemose, shorter than leaves, entirely glabrous; bracts and ochreolae glabrous, minute; nodules 1- to 3-flowered. Fruiting pedicels stout, 2.5 to 3.5 mm. long. Fruits smooth, yellow (Schipp), ovoid, 11 to 12 mm. long, 7 to 9 mm. in diam., apex obtusely apiculate, crowned by the persistent perianth lobes, contracted slightly at base.

Type in the Herbarium of the University of Michigan, *W. A. Schipp 1200*, collected on hilltop in forest shade, Jacinto Hills, Toledo District, British Honduras, Aug. 28, 1933. Duplicates in Gray Herbarium and Field Museum Herbarium.

C. lancifolia is near *C. laurifolia* Jacq., but differs in its small lanceolate pointed leaves.

Coccoloba laurifolia Jacq., Hort. Schoenbr. 3: 9, t. 267. 1798. This species, widely distributed from Florida through the West Indies to Venezuela, apparently has not been recorded from Central America. Two collections, referable here, are at hand from northern British Honduras: *Percy H. Gentle 231* (F, M), Corozal District, 1931–1932; *C. L. Lundell 4945* (F, M), in high ridge, Consejo, Corozal District, Aug. 30, 1933. Locally it is known as "wild grape."

Coccoloba Schippii sp. nov.—Arbor, 10 m. alta, 15 cm. diam. Ramuli glabri, striati. Folia petiolata, petiolo 9–14 mm. longo, glabra, chartacea, lanceolata, 8–12.5 cm. longa, 3–5 cm. lata, apice longe acuminata, basi rotundata vel anguste rotundata, minute reticulato-venosa. Inflorescentiae terminales vel laterales, ut videtur spicatae, rachidibus puberulis, nodulis 1–floris; bracteae ovato-oblongae, ca. 1 mm. longae, extus hirsutae; ochreolae bracteam superantes. Alabastra sessilia vel subsessilia, glabra.

A tree 15 cm. in diam., 10 m. high; branchlets slender, entirely glabrous, striate, drying black. Stipules sheathing, barbate at apex, glabrous otherwise, petiole basal. Leaf blades entirely glabrous, chartaceous, lanceolate, 8 to 12.5 cm. long, 3 to 5 cm. wide, apex long acuminate, base rounded or narrowed and rounded, costa prominent beneath, slightly elevated above, main lateral veins 6 or 7 on each side, prominulous beneath, slightly less conspicuous above, minutely reticulate-veined on both surfaces. Petioles slender, drying black, glabrous, canaliculate, 9 to 14 mm. long. Inflorescence terminal or lateral, 2.5 to 4.5 cm. long (in bud), apparently spicate; rachis puberulent, hirsute at base of bracts; nodules 1–flowered; lower bract 2 mm. long, clawed, upper bracts ovate-oblong, about 1 mm. long, hirsute on outside; ochreolae campanulate, thin, with rounded lobes, exceeding the upper bracts, up to 1.8 mm. long, puberulent on outside, bearing some longer hairs. Flower buds sessile or subsessile, glabrous; perianth lobes ovate or elliptic, rounded at apex. Stigmas 3.

Type in the Herbarium of the Field Museum of Natural History, No. 733,663, *W. A. Schipp S–687*, collected in forest shade at Camp 31 of the British Honduras-Guatemala boundary survey, in Toledo District, British Honduras, Mar. 18, 1934; alt. about 675 m.; fragment of type and a photograph in the Herbarium of the University of Michigan.

C. Schippii appears to be related to *C. guyanensis* Meissn. of South America.

Coccoloba spicata sp. nov. (fig. 4).—Arbor, 5–16 m. alta, 10–20 cm. diam. Ramuli glabri. Folia petiolata, petiolo 1–2.3 cm. longo, coriacea, supra glabra, subtus ad costam et in axillis pilosa, late ovata vel oblongo-elliptica, 6.5–15 cm. longa, 4–10 cm. lata, apice anguste rotundata, obtusa, vel late

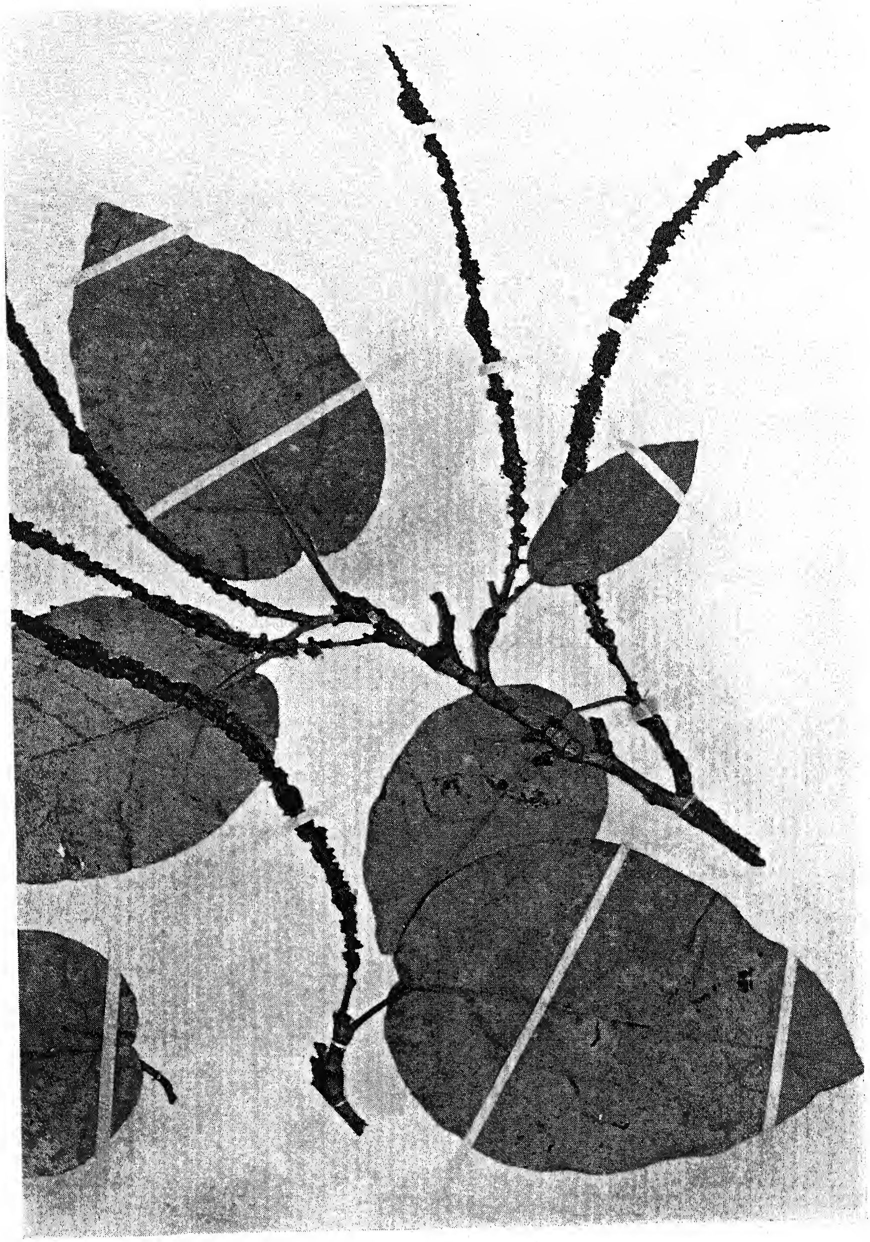

Fig. 4. *Coccoloba spicata* Lundell. Type (*Lundell and Lundell 7325*), in Herbarium of the University of Michigan. $\times \frac{1}{2}$.

obtuse apiculata, basi late rotundata, cordata vel emarginata. Inflorescentiae terminales, spicatae, 8.5–25 cm. longae, rachidibus glabris vel puberulis, nodulis 1–2–floris; bracteae hirtellae, 1–1.2 mm. longae; ochreolae bracteam aequantes vel superantes, hirtellae, apice barbatae. Flores et fructus sessiles. Perianthii tubus ca. 1 mm. longus, lobis late ovatis vel suborbicularibus, ca. 2 mm. longis. Ovarium ca. 1 mm. longum, ut videtur abortivum. Styli 3. Fructus late ovoideus vel subglobosus, ca. 7 mm. longus, 6 mm. diam., apice basique rotundatus, obscure costatus.

A tree, 10 to 20 cm. in diam., 5 to 16 m. high; branchlets glabrous. Stipules lax, usually 5 to 9 mm. long, sometimes larger, rufous hirsute at first, glabrescent early, petioles usually basal, sometimes medial to subapical. Leaf blades barbate beneath in the axils of the primary veins and short hairy along the costa, glabrous otherwise, coriaceous to rigidly coriaceous, broadly ovate or oblong-elliptic, 6.5 to 15 cm. long, 4 to 10 cm. wide, juvenile blades up to 29 cm. long, 21 cm. wide, apex slightly narrowed and rounded, obtuse, or broadly obtuse apiculate, base broad and round, deeply cordate to emarginate, costa prominent beneath, thick at base, less conspicuous above, primary veins 5 to 7 on each side, prominent on undersurface, less conspicuous above, veinlets scarcely evident above, minutely but obscurely reticulate below. Petioles thick, puberulent at top above, otherwise glabrous, 1 to 2.3 cm. long. Inflorescence terminal, spicate, 8.5 to 25 cm. long; rachis glabrous or puberulent; nodules 1– or 2–flowered; bracts hirtellous, ovate-triangular, rounded, 1 to 1.2 mm. long; ochreolae equaling or exceeding bracts, hirtellous, sometimes barbate at apex. Flowers and fruits sessile, crowded. Perianth pale green usually glabrous, sometimes puberulent, the tube about 1 mm. long; lobes broadly ovate or suborbicular, about 2 mm. long. Filaments about 2 mm. long. Ovary trigonal, about 1 mm. long (abortive?); styles 3. Fruits (*Lundell 560*) broadly ovoid or subglobose, about 7 mm. long and 6 mm. in diam., apex and base rounded, slightly costate.

Type in the Herbarium of the University of Michigan, *C. L. Lundell and Amelia A. Lundell 7325*, collected in young legume thicket around Sacred Cenote, Chichen Itza, Yucatan, Mexico, May 13, 1938.

Additional specimens examined: MEXICO: Yucatan, Izamal, Sept., 1895, *G. F. Gaumer 819* (F). Kancabtsonot, May, 1917, *Gaumer and sons 23894* (F). Without locality, 1917–1921, *Gaumer 23976* (F, NY). Chichen Itza, June 28, 1929, *J. Bequaert 103* (F). Valladolid, 1935, *Ramon S. Flores* (F). Without locality, 1937, *Morris Steggerda 1B* (F). Quintana Roo, Coba, in relic deciduous forest east of ruins, July 4, 1938, *Lundell and Lundell 7813* (M). BRITISH HONDURAS: Corozal District, Santa Rita, in *acahual*, Sept. 14, 1933, *Lundell 4951* (F, M, NY). Orange Walk District, Honey Camp, Oct., 1929, *Lundell 560* (F, NY).

Distribution: In dry deciduous upland forest of Yucatan, Quintana Roo, and northern British Honduras.

Vernacular names: "bob" (*Lundell and Lundell 7813, Flores* in 1935); "xbobche" (*Gaumer 819*); "boob" (*Steggerda 1B*); "wild grape" (*Lundell 4951*).

Economic uses: The large juvenile leaves are utilized in Valladolid for wrapping a sweet called "mercocha" (*Flores*).

The species is related to *C. mayana* Lundell. A collection from Champoton, Campeche, *Flores* in 1934 (F), evidently taken from a tree cultivated for shade, locally known as "bochiche," may be referable here. It differs most obviously from *C. spicata* in having slender puberulent branchlets and oblong leaves.

Heliocarpus horridus sp. nov.—Arbor parva, 5-metralis, omnino persistenter minute rufo-glandulosa. Folia integra, late ovata vel suborbicularia, 7–15.5 cm. longa, 4–10.3 cm. lata, apice caudato-acuminata, basi subcordata, serrata, supra parce hirsuta, subtus breviter stellato-hirsuta; petiolis 2.7–4 cm. longis, supra hirsutis. Infructescentiae parvae, rachidibus hirsutis et dense glandulosis. Pedicelli fructiferi 4–4.5 mm. longi. Fructus crasse stipitatus.

A small tree 5 m. high; all parts clothed with minute reddish glands, blackish with age; branchlets covered with glands, glabrous otherwise. Leaves integral, thin, broadly ovate or suborbicular, 7 to 15.5 cm. long, 4 to 10.3 cm. wide, apex caudate-acuminate, base subcordate, serrate, teeth obtuse, the basal glandular, upper surface sparsely hirsute with simple or few-branched hairs, lower surface short hirsute with denser stellate hairs, palmately 5-veined; petioles 2.7 to 4 cm. long, hirsute above, densely so at base of blade. Panicles small, the branches hirsute and densely glandular. Fruiting pedicels 4 to 4.5 mm. long, jointed at the middle. Fruits with stout stipe 4 to 5 mm. long; body ellipsoid, the faces deeply rugose, sparingly hirsute, bearing 3 to 6 plumose bristles subequaling those of fringe; plumose bristles of fringe as much as 6.5 mm. long, extending down the stipe.

Type in the Herbarium of the University of Michigan, *C. L. Lundell and Amelia A. Lundell 7821*, collected in relic forest east of Coba, Quintana Roo, Mexico, July 5, 1938; vernacular name "holol."

H. horridus is noteworthy primarily for the long plumose bristles on the faces of the fruits. The abundant minute reddish or blackish glands covering all parts, the broad ovate leaves rather sparsely short hirsute on both surfaces, the fruiting pedicels jointed at the middle, and the small panicles distinguish it further. It is related to *H. glanduliferus* Rob.

Cassipourea belizensis sp. nov.—Arbor, 25 cm. diam.; ramulis crassiusculis, strigillosis. Folia petiolata, petiolo 3–8 mm. longo, strigilloso, late elliptica, 4.5–8.5 cm. longa, 2.6–5.5 cm. lata, apice abrupte subacuminata, acuta vel obtusa, basi late cuneata, subcoriacea, integra, venis lateralibus 5–7. Flores fasciculati, pedicellis strigillosis, usque ad 4 mm. longis. Calyx abrupte stipitatus, glaber vel subglaber, tubo ca. 3 mm. longo, quinquelobato, lobis ovatis, 1.7–2 mm. longis. Petala ca. 7.5 mm. longa, villosa. Stamina usque ad 5.5 mm. longa. Ovarium 3–loculare.

A tree, diam. 25 cm.; branchlets rather stout, at first covered with short appressed hairs, glabrescent early. Leaves petiolate, the petioles stout, grooved, 3 to 8 mm. long, short appressed hairy, the blades broadly elliptic, 4.5 to 8.5 cm. long, 2.6 to 5.5 cm. wide, apex abruptly subacuminate, acute or obtuse, base broadly cuneate, subcoriaceous, with a few appressed short hairs at base and along margin, glabrous otherwise, entire or essentially so, costa prominent beneath, slightly raised above, main lateral veins 5 to 7, veins and veinlets prominulous. Fowers fascicled, distinctly stalked. Pedicels appressed hairy, up to 4 mm. long (not including stipe). Calyx abruptly contracted at base into a stipe about 1 mm. long, with a few appressed hairs outside or entirely glabrous, tube about 3 mm. long, 5–lobed, the lobes deltoid-ovate, 1.7 to 2 mm. long, sericeous within, short tomentose at apex along margin of lobes. Petals about 7.5 mm. long, the blade short villous on both surfaces, the fringe villous. Stamens up to 5.5 mm. long. Ovary depressed-globose, glabrous below, sericeous above, 3–celled. Style sericeous.

Type in the Herbarium of the University of Michigan, *Percy H. Gentle 2749*, collected in *acahual* near Sarawee Pine Ridge, Stann Creek District, British Honduras, April 13, 1939; vernacular name "waterwood."

From the other British Honduran species, identified by P. C. Standley as *C. podantha* Standl., *C. belizensis* differs conspicuously in leaf form. In *C. podantha* the leaves are much narrower, long acuminate, and often distinctly toothed. In *C. belizensis* the blade of the petals is short villous whereas it is quite glabrous in the other species.

Turpinia tricornuta sp. nov.—Arbor; ramulis crassis. Folia pinnata, petiolata, petiolo usque ad 6 cm. longo; foliola glabra, coriacea, 5 vel 7, raro 2, 3 vel 4, oblongo-elliptica vel ovato-elliptica, 4.5–13.5 cm. longa, 2.4–7 cm. lata, apice abrupte acuminata, basi rotundata, serrata, venis lateralibus 6–9. Inflorescentiae axillares, paniculatae, pauciflorae, usque ad 8.5 cm. longae. Pedicelli crassi, minute puberuli, usque ad 6 mm. longi. Sepala ciliolata, inaequalia, 3 exteriora late ovata vel elliptica, 2.5–5 mm. longa, 2 interiora late elliptica vel obovato-elliptica, 5.5–7 mm. longa. Petala obovato-spathulata, 5–6.5 mm.

longa, intus parce pilosa, basi ciliata, apice eroso-ciliolata. Filamenta crassa, usque ad 5.2 mm. longa, 1 mm. lata, glabra. Ovarium villosum. Fructus ad mediam tricornutus.

A tree; branchlets thick, terete, reddish, minutely and sparsely puberulent around the nodes at first, glabrous early, the bark scaling off longitudinally. Leaves opposite, pinnate, petiolate, the petioles up to 6 cm. long, terete; petiolules of lateral leaflets up to 1.8 cm. long, canaliculate; leaflets usually 5 or 7, sometimes 2, 3 or 4, oblong-elliptic or ovate-elliptic, 4.5 to 13.5 cm. long, 2.4 to 7 cm. wide, apex abruptly acuminate, base often inaequilateral, usually rounded, sometimes rounded and abruptly acutish, entirely glabrous, coriaceous, serrate, costa prominent beneath, raised above as a fine narrow line or nearly plane, main lateral veins 6 to 9 on each side, widely arcuately ascending, prominulous on under surface. Inflorescence axillary, paniculate, small, few-flowered, up to 8.5 cm. long, usually not exceeding the petiole, sparsely and very minutely puberulent. Pedicels stout, minutely and sparsely puberulent, up to 6 mm. long, jointed at base. Sepals unequal, rather thick, ciliolate, the three outer broadly ovate or elliptic, 2.5 to 5 mm. long, the two inner broadly elliptic to obovate-elliptic, 5.5 to 7 mm. long. Petals obovate-spathulate, clawed, 5 to 6.5 mm. long, hairy along the midvein inside, the basal half ciliate, the upper half erose-ciliolate. Filaments thick, up to 5.2 mm. long, 1 mm. wide; anthers cordate, about 1.5 mm. long, blunt at apex. Disk shallowly lobed. Ovary villous, 3-celled at base, the carpels free above; the 3 styles united at apex, free below. Drupe tricornute almost to the middle, the lobes divaricate, thick at base, tapering to the persistent style.

Type in the Herbarium of the University of Michigan, *Eizi Matuda 2941*, collected on north side of Mt. Tacana, Chiapas, Mexico, April 2, 1939; alt. 2100 m.

The large coriaceous leaflets, small few-flowered narrow panicles of comparatively large flowers, ciliate petals, villous ovary, and the tricornute drupes mark the species. Its affinity is with *T. occidentalis* G. Don.

Ternstroemia impressa sp. nov.—Arbor 10–12 m. alta, 30 cm. diam. Folia rubra, glabra, petiolata, petiolo 4–6 mm. longo, oblanceolata vel obovata, 3.5–6.5 cm. longa, 1.5–3 cm. lata, apice emarginata, late obtusa vel rotundata, basi cuneata, obscure serrulata, revoluta, coriacea, venis supra impressis. Pedicelli 2.3–3.5 cm. longi. Sepala late ovata, 6.5–8 mm. longa.

A tree 10 to 12 m. high, 30 cm. in diam.; branchlets stout, rather short, with leaves usually crowded at apex. Leaves red, glabrous, alternate, petiolate, the petioles stout, 4 to 6 mm. long, the blades oblanceolate or obovate, 3.5 to 6.5 cm. long, 1.5 to 3 cm. wide, apex emarginate, bluntly obtuse or rounded, base cuneate, very obscurely serrulate, revolute, rigidly coriaceous, lateral veins obscure below, the costa, veins and veinlets conspicuously im-

pressed above. Pedicels 2.3 to 3.5 cm. long, enlarged below the calyx, tapering to a slender base. Bractlets inserted at base of calyx, triangular, about 3 mm. long, deciduous. Sepals broadly ovate, 6.5 to 8 mm. long, margin of outer ones glandular-denticulate. Young fruits acute.

Type in the Herbarium of the University of Michigan, *Eizi Matuda 2814*, collected at Chiquihuite, Mt. Tacana, Chiapas, Mexico, March 27, 1939; alt. 2800 m.

T. impressa is noteworthy for the small thick rigidly coriaceous red leaves with veins prominently impressed above.

Styrax magnus sp. nov.—Arbor magna, 15–17 m. alta, 50–55 cm. diam. Ramuli ferrugineo-stellato-tomentosi. Folia alterna, petiolata, petiolo 1.4–2.8 cm. longo, chartacea, obovata vel elliptica, 12–20 cm. longa, 7–11.5 cm. lata, apice breviter acuminata, basi acutiuscula, supra nervis venisque stellato-pilosis, impressis, subtus albido-stellato-tomentosa, nervis lateralibus 10–12. Inflorescentiae axillares vel terminales, paniculatae, usque ad 10 cm. longae, ferrugineo-tomentosae. Pedicelli usque ad 12 mm. longi. Calyx ca. 3.5 mm. altus, tomentosus, quinquedentatus. Corolla 16 mm. longa, extus sericea, lobis valvatis, oblongis, ca. 11 mm. longis, 4 mm. latis. Stamina 10. Filamenta stellato-pilosa. Ovarium multiovulatum. Fructus ellipsoideus, ca. 18 mm. longus, 12 mm. diam.

A tree 15 to 17 m. high, 50 to 55 cm. in diam.; branchlets stout, ferruginous-tomentose with stellate hairs. Leaves alternate, the petioles stout, tomentose, 1.4 to 2.8 cm. long, the blades chartacous, obovate or elliptic, 12 to 20 cm. long, 7 to 11.5 cm. wide, apex abruptly short acuminate to rounded, base slightly narrowed, acutish, subentire, persistently stellate-pilose above along the impressed costa and main lateral veins, glabrescent otherwise, under surface white tomentose with minute close indument and a coarser thinner stellate-pilose layer, main lateral veins 10 to 12 on each side, prominulous beneath, veinlets reticulate. Inflorescence axillary or terminal, paniculate, many-flowered, pedunculate, up to 10 cm. long, ferruginous-tomentose with stellate hairs. Pedicels up to 12 mm. long. Calyx white tomentose and bearing a few coarser rusty stellate hairs, cupuliform, about 3.5 mm. long, minutely 5–denticulate. Corolla about 16 mm. long, sericeous outside, the tube 4 to 5 mm. long, the lobes valvate, oblong, about 11 mm. long, 4 mm. wide, acutish, short pilose at apex. Stamens 10, shorter than corolla, the filaments stellate-pilose. Ovary stellate-pilose, 3–celled, ovules numerous. Style slender, about 11 mm. long, glabrous. Fruits ellipsoid, about 18 mm. long, 12 mm. in diam.

Type in the Herbarium of the University of Michigan, *Eizi Matuda 2982*, collected on north side of Mt. Tacana, Chiapas, Mexico, Apr. 2, 1939; alt. 2100 m.

S. magnus is referable to the section Eustyrax, series Valvatae in Perkins' monograph in the Pflanzenreich. Evidently it has affinity with *S. argenteus* from which it may be readily distinguished by the larger obovate or elliptic leaves, paniculate inflorescence up to 10 cm. long, differences in the corolla, and larger fruits.

Symplocos tacanensis sp. nov.—Arbor 8–10 m. alta, 30 cm. diam.; ramulis crassiusculis, hirsutis. Folia chartacea, flavescentia, oblonga vel oblongo-elliptica, 5–12 cm. longa, 2.5–5 cm. lata, apice abrupte acuminata, basi subcordata vel rotundata, subtus parce rufo-pilosa, minute denticulata. Petioli 4–8 mm. longi. Flores rosei in fasciculis sessilibus vel subsessilibus. Calycis tubus ca. 2 mm. longus, strigosus, lobis 5, ovatis, 3–3.5 mm. longis, strigosis, ciliatis. Corolla 13–14 mm. longa, lobis ciliolatis. Ovarium 3– vel 4–loculare, pilosum; stylus pilosus, 10–10.5 mm. longus. Fructus ellipsoideus, 17–20 mm. longus, 12–13 mm. diam., parce hirsutus.

A tree 8 to 10 m. high, 35 cm. diam. Branchlets rather stout, densely hirsute, the hairs reddish-brown. Leaves chartaceous, yellowish, oblong or oblong-elliptic, 5 to 12 cm. long, 2.5 to 5 cm. wide, apex abruptly short acuminate, base subcordate or rounded; appressed rufous-hairy above at first, glabrous with age; under surface persistently rufous-pilose, densely so along the prominent midrib; costa, veins, and veinlets impressed above, the main lateral veins 6 to 9 on each side, prominulous below, openly reticulate; margin obscurely and rather remotely denticulate with minute red subappressed glandular teeth. Petioles sulcate, hirsute, 4 to 8 mm. long. Flowers sessile, borne in dense sessile or subsessile hirsute fascicles at leafless nodes. Bracts ovate, rufous-brown, strigose. Calyx rufous-brown, strigose, the tube about 2 mm. long; the lobes 5, ovate, 3 to 3.5 mm. long, strigose and ciliate. Corolla 13 to 14 mm. long, the lobes adherent to stamen tube, connate below, obovate-oblong, rounded, ciliolate above the middle, each lobe with a small sericeous area below apex, the corolla entirely glabrous otherwise. Stamens slightly shorter than corolla, apparently in 5 series, glabrous, filaments united into a tube, free and complanate above. Ovary 3– or 4–celled, densely pilose; style 10 to 10.5 mm. long, densely pilose below, nearly glabrous above. Fruits ellipsoid, 17 to 20 mm. long, 12 to 13 mm. in diam., sparsely hirsute.

Type in the Herbarium of the University of Michigan, *Eizi Matuda 2976*, collected on north side of Mt. Tacana, Chiapas, Mexico, April 2, 1939; alt. 2100 m.

S. tacanensis, referable to Brand's subgenus Eusymplocos, section Symplocastrum, apparently belongs to the subsection Pseudalstonia in which it has affinity with *S. pycnantha* Hemsl. and *S. prionophylla* Hemsl. The copious rufous-brown coarse pubescence and the yellowish leaves immediately distinguish it from both of these.

Bouvardia venosissima sp. nov.—Ramuli graciles. Stipulae subulatae, 2–5.5 mm. longae. Folia opposita, subsessilia, membranacea, ovata vel ovato-lanceolata, 2.5–10 cm. longa, 1.7–5.5 cm. lata, apice attenuato-acuminata, basi subcordata vel rotundata, ciliata, striolata, prominente reticulata, venosissima. Inflorescentiae glabrae, axillares vel terminales, cymoso-corymbosae. Pedicelli 3–5 mm. longi. Calyx 4-lobatus, lobis subulatis, 1.8–2.6 mm. longis, apice ciliatis. Corolla rubra, striolata, extus glabra, intus ad basin villosa, tubo 9–11 mm. longo, lobis ovatis, ca. 3.5 mm. longis. Stamina inclusa. Capsula ca. 5 mm. diam., striolata.

Branchlets slender, striolate, at first somewhat compressed and conspicuously bisulcate with a few hairs scattered along the margins of the grooves, glabrous and terete with age. Stipules at first sparsely pilose at base, soon glabrous, subulate, 2 to 5.5 mm. long, short-laciniate. Leaves opposite, subsessile, the petiole up to 1.5 mm. long, the blades membranaceous, ovate or ovate-lanceolate, 2.5 to 10 cm. long, 1.7 to 5.5 cm. wide, apex attenuate-acuminate, base subcordate or rounded, ciliate, glabrous otherwise, striolate, conspicuously reticulate-veined on both surfaces, main lateral veins 4 to 6 on each side, pinnate, strongly arcuately ascending, anastomosing, the costa and veins slightly impressed above. Inflorescence glabrous, axillary and terminal, cymose-corymbose, usually many-flowered. Pedicels slender, 3 to 5 mm. long, becoming 7 mm. long in fruit. Hypanthium glabrous, about 1 mm. long. Calyx lobes subulate, 1.8 to 2.6 mm. long, usually ciliate at apex, glabrous otherwise. Corolla reddish, glabrous outside, striolate, the tube 9 to 11 mm. long, with a villous ring within near the base, the lobes ovate, about 3.5 mm. long. Anthers included, 2.5 to 3 mm. long. Style included or shortly exserted. Capsule about 5 mm. wide, striolate.

Type in the Herbarium of the University of Michigan, *Eizi Matuda 2748*, collected along border of Guatemala on Mt. Tacana, Chiapas, Mexico, Mar. 17–23, 1939; alt. 1400 m.

Additional specimens examined: MEXICO: Chiapas, Mt. Tacana, Aug., 1938, alt. 1000–2000 m., *Matuda 2464*; on north side of Mt. Tacana, April 2, 1939, alt. 2100 m., *Matuda 2954*.

B. venosissima has affinity with *B. dictyoneura* Standl., but differs, according to description, in its larger ciliate subcordate leaves and shorter calyx lobes ciliate at apex. All parts of the plant are minutely striolate, a noteworthy peculiarity. *Matuda S–157* and *860* from Mt. Ovando, Chiapas have been identified by Dr. P. C. Standley as *B. dictyoneura*, and I have interpreted this species on the basis of these collections. The Matuda material of *B. dictyoneura* does not have reticulate-veined leaves, a characteristic of this species according to the original description.

Rondeletia tacanensis sp. nov.—Frutex. Ramuli crassiusculi, pubescentes. Stipulae triangulares, 5–9 mm. longae, cuspidatae. Folia elliptica, 11.5–22 cm. longa, 7–11.5 cm. lata, apice acuminata, basi late cuneata, subtus novellis tomentosa. Petioli 1–3 cm. longi. Inflorescentiae terminales, pedunculatae, thyrsiformes, paniculatae, usque ad 30 cm. longae. Calyx 4-lobatus, lobis 3.2–7 mm. longis. Corollae tubus 17–18 mm. longus; lobi oblongi vel ovato-oblongi, 3.5–5 mm. longi, extus basi strigosi, intus glabri.

A shrub 3 to 4 m. high, 10 to 15 cm. in diam.; branchlets rather stout, subangulate, densely short hairy. Stipules triangular, 5 to 9 mm. long, rather abruptly cuspidate, erect, persistent. Leaves opposite, the petioles 1 to 3 cm. long, the blades elliptic, widest above the middle, 11.5 to 22 cm. long, 7 to 11.5 cm. wide, apex abruptly acuminate, base broadly cuneate, at first densely tomentose on under surface, with age sparsely so, the costa persistently hairy, upper surface bearing a few persistent hairs, main lateral veins 12 to 14 on each side, prominulous beneath, arcuately ascending. Inflorescence terminal, pedunculate, the flowers sessile in small crowded cymules, these sessile or pedunculate, arranged in narrow thyrsiform panicle up to 30 cm. long. Bracts subulate, 5 to 7 mm. long. Hypanthium densely pubescent with ascending subappressed short hairs, 2.5 to 2.9 mm. long. Calyx lobes 4, subulate, unequal, 3.2 to 7 mm. long, suberect. Corolla tube slender, 17 to 18 mm. long, nearly glabrous, bearing only a few hairs, these mostly at apex, naked in the throat, pilose at base within, the 4 lobes oblong or ovate-oblong, 3.5 to 5 mm. long, up to 4 mm. wide, spreading, undulate, glabrous within, strigose outside below. Apex of anthers exserted. Style included.

Type in the Herbarium of the University of Michigan, *Eizi Matuda 2928*, collected on west side of Mt. Tacana, Chiapas, Mexico, Mar. 30, 1939; alt. 2800 m.

Another collection from the same locality, *Matuda 2396*, is tentatively referred here. The leaves are pilose with spreading hairs on lower surface rather than tomentose, the branchlets and rachis of the infructescence are densely short hirsute, the panicle is as much as 45 cm. long, and the capsules are hairy, about 6.5 mm. long. This may represent a variety.

R. tacanensis belongs to the section Laniflorae (N. Amer. Fl. 32: 45. 1918), but does not appear close to any of the described species. The large leaves and very long panicles crowded with flowers are noteworthy.

Viburnum chiapense sp. nov.—Arbor 7 m. alta, 15–20 cm. diam. Ramuli crassiusculi, dense tomentosi, pilis stellatis flavescentibus. Folia ovata vel ovato-elliptica, usque ad 16.5 cm. longa, 11 cm. lata, apice acuminata, basi late rotundata et emarginata, dentata, supra parce stellato-pilosa, subtus stellato-tomentosa. Petioli usque ad 2.5 cm. longi. Pedunculi dense tomentosi, 6–7.5 cm.

longi. Cymae radii stellato-tomentosae. Calycis tubus stellato-tomentosus, usque ad 3 mm. longus, lobis ca. 1 mm. longis. Corolla campanulata, 4–5 mm. longa, extus parce strigosa. Stylus glaber.

A tree 7 m. high, 15 to 20 cm. in diam.; branchlets rather stout, terete, tawny, densely tomentose with fine stellate hairs. Leaves opposite, petiolate, the petiole up to 2.5 cm. long, densely stellate-pubescent; blades ovate or ovate-elliptic, up to 16.5 cm. long and 11 cm. wide, apex acuminate, base broadly rounded and emarginate, conspicuously dentate above the middle, the teeth gland-tipped, thinly stellate-pubescent above with sessile hairs, paler beneath, finely stellate-tomentose, the hairs substipitate or sessile, primary veins 5 or 6, strongly ascending, conspicuous on under surface. Peduncle 6 to 7.5 cm. long, tomentose like branchlets. Bracts at base of inflorescence linear, short. Cyme large, up to 11 cm. wide, 6.5 cm. long, usually 4 times compound, the primary rays 5 or 6, up to 3.5 cm. long, tomentose, secondary rays up to 1.7 cm. long. Bractlets at base of flowers linear, stellate-pubescent. Flowers sessile. Calyx tube up to 3 mm. long, stellate-tomentose, the lobes usually triangular, about 1 mm. long, stellate-pubescent. Corolla campanulate, 4 to 5 mm. long, lobed to the middle, sparsely short strigose externally with straight simple hairs. Filaments about 5 mm. long. Style glabrous. Dry fruit ovoid, about 6.5 mm. long, about 5 mm. in diam., sparsely stellate-pubescent, not conspicuously grooved, the intrusion pronounced, extending almost to the center.

Type in the Herbarium of the University of Michigan, *Eizi Matuda 2925*, collected on west side of Mt. Tacana, Chiapas, Mexico, Mar. 30, 1939; alt. 2800 m.

V. chiapense, referable to the section Disjuncta of Morton (Contr. U. S. Nat. Herb. 26: 342. 1933), is related to *V. disjunctum* Morton and *V. jucundum* Morton. From *V. disjunctum*, *V. chiapense* may be separated by its ovate conspicuously dentate leaves, calyx tube almost three times as long, calyx lobes twice as long, and much larger corolla. *V. jucundum* bears a close resemblance, but differs at once in its stellate-pubescent smaller corolla, short peduncle, and less conspicuously toothed smaller leaves.

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Some Incorrectly Described Asclepiads

Roland M. Harper

(with two figures)

Many or most of the plant descriptions in our manuals seem to have been written by persons who either have never seen the species growing, or else have collected them on hurried trips, along with many other plants, without taking time to study them until after they were pressed. In this way important characteristics of the living plants that are obscured by the drying and pressing process are often overlooked; and this is especially true of fruits and seeds, which are collected less frequently than flowers.[1]

An interesting case of this is the southern swamp milkweed, *Asclepias perennis.* That species was described by Thomas Walter in his Flora Caroliniana in 1788, and later named *A. parviflora* by Aiton (who perhaps was unaware at the time of Walter's description) in 1789, and *A. debilis* by Michaux in 1803. Its present known range is in alluvial swamps from Georgia (and perhaps South Carolina) to Louisiana (and perhaps Texas) in the coastal plain, and inland in the Mississippi valley to the Wabash bottoms of Indiana. Although apparently all our Asclepiadaceae are perennials, the name Walter selected for this species was probably suggested by the fact that its stem generally has one or two stubs of dead trunks near the base, presumably indicating that it does not die down completely to the ground in winter, and puts out a new stem from a little above the ground in spring. The stem is rather tough, and although it would hardly be called woody, the plant might be classed as a short-lived shrub.

There is quite a long description of it in Elliott's Botany of South Carolina and Georgia 1: 323–324. 1817), under the name of *A. parviflora* (with *A. perennis* and *A. debilis* given as synonyms); but Elliott, like his predecessors, said nothing about its fruit or seeds.

The next important treatment is that of Chapman (Fl. So. U. S., 365. 1860), who used Walter's name, *perennis,* and gave *parviflora* and *debilis* as synonyms. He made it the last species in the genus, and distinguished

[1] For an illustration of an important fruit character that is wholly obscured in dried specimens see my note on *Kneiffia,* in the Plant World, 8: 301–303. "Dec. 1905." [Jan. 1906.] The character there described furnishes an additional means of separating *Kneiffia* from *Oenothera,* which was disregarded by Munz in his revision of *Kneiffia* a few years ago (Bull. Torrey Bot. Club 64: 287–306. 1937). *Kneiffia* had long been known to differ from *Oenothera* in having its flowers open all day, instead of at night, but in spite of that some member of the Plant World editorial staff, thinking only of *Oenothera,* attempted to make my article more "popular" by inserting the inapplicable common name "evening primrose" without my knowledge or consent.

from the 18 others, in his key, by the words "Stem shrubby: seeds mostly naked." In the description the only statement about the fruit is "follicle ovate-lanceolate, smooth;" and there is no further mention of the seeds.

The next edition of Gray's Manual after that, the fourth, dated 1863, calls our plant *A. parviflora* again, and says "Coma of the seeds wanting;" and that was repeated in various later editions.

Britton and Brown's Illustrated Flora (3: 12. 1898) describes it as *A. perennis* Walt. (with no synonyms), allies it most closely with *A. brachystephana* Engelm., a Great Plains species, and says of it in part: "follicles glabrous, erect on the erect fruiting pedicels; seeds . . . . very thin, destitute of coma." This seems to be the beginning of a misstatement about the fruit that has been current ever since; but the description of the seeds is correct enough.

Small, in his Flora of the Southeastern United States, 1903, recognized 30 species of *Asclepias*, and put *A. perennis* near the middle of the genus, between *A. Curassavica* and *A. Texensis*, in a group of 12 species characterized by "follicles erect on erect fruiting pedicels." In his key one of the distinguishing characteristics for this species was "seeds destitute of coma" (a fact not easily ascertained at flowering time). In the description the statement about follicles was repeated from the key, but the seeds were said to be "1–1.5 mm. long . . . . apparently destitute of coma." (The "mm." was evidently a misprint for cm.)

In his Manual of the Southeastern Flora, thirty years later, *A. perennis* is put with *A. incarnata* and *A. pulchra* (two northern bog or marsh species which were formerly regarded as only varietally distinct from each other, and which I have never seen in the South) in the section *Incarnatae;* and that and two other sections are characterized in the key by "follicles erect on erect pedicels." In neither key nor description is there any mention of whether the seeds are comose or not (as if he was not sure about that), but the length of the seed is given as 9–12 mm. (In only one other of the 24 species of *Asclepias* recognized in that book is the size of the seeds mentioned, and that is *A. quadrifolia,* the next species, with seeds 5–6 mm. long.)

In Robinson and Fernald's Manual (the so-called 7th edition of Gray's) for the northeastern states (1908), *Asclepias perennis* is one of four species characterized in the key by "follicles and pedicels erect." In the description (p. 656) there is no further mention of the fruit, but the seeds are said to be "sometimes destitute of a coma!" (The exclamation point is part of the quotation.)

Prof. Fernald writes me that the several ambiguous statements about the seeds, that I have quoted, may be based on *Asclepias texana* Heller, which was described by Gray in 1876 as *A. perennis* var. *parvula* (raised to a species by Miss Vail in 1899), and was regarded by his suc-

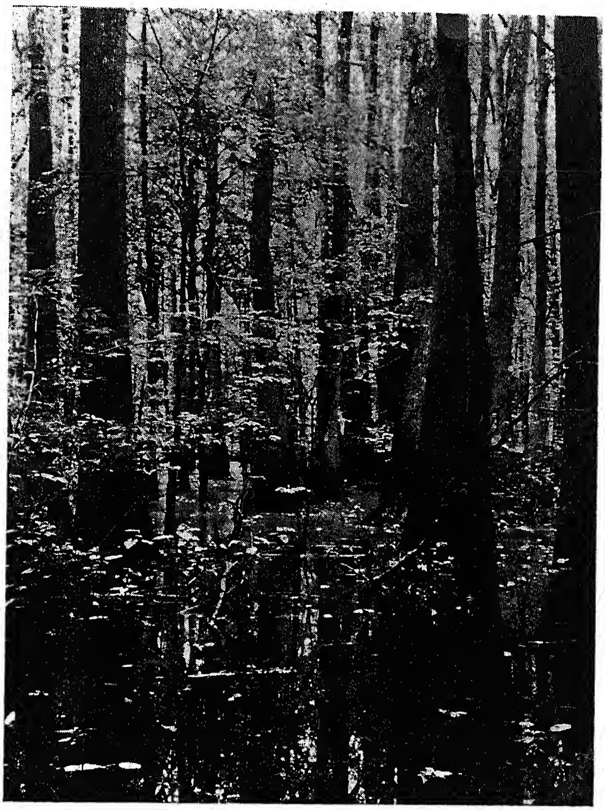


Fig. 1. Goose Pond, a tupelo gum slough in bottoms of Warrier River about six miles west-southwest of Tuscaloosa. July 30, 1938. No specimens of *Asclepias perennis* appear in the view, but it was collected in a similar place in the same slough a few weeks later, when the water had receded.

cessors as doubtfully distinct, though accepted as a good species by Small in 1903. That species seems to be known only from a few old specimens from Texas, and is said to resemble *A. perennis* in having a stem woody at the base, and rather large reddish seeds, but the follicles are apparently erect, and the seeds comose as in most other species of the genus. It very likely grows in open places, where the seeds are readily transported by the wind (as in the Asclepiadaceae generally), while *A. perennis* frequents dense shady swamps.

Herbarium specimens of any or all species of *Asclepias* usually represent the flowering stage only, for the flowers are rather showy, and differ perceptibly in every species. And as botanists are not very numerous within the range of *A. perennis*, it is not surprising that its fruiting stage

Fig. 2. Some typical fruiting specimens of *Asclepias perennis*, collected in and around Goose Pond, Sept. 7, 1938, and photographed in the office a few hours later, before pressing. Some loose seeds are also shown. The scale indicates inches.

should have been so long misunderstood. I have known the species since 1901, but never saw its fruit until June 28, 1933, and only one or two follicles then, in the bottoms of the Warrior River in Tuscaloosa County, Alabama. That was a little early for fruit, but one of the specimens collected at that time (no. 3079) shows a follicle nearly grown. I noticed

then that the follicles are by no means erect on erect pedicels, as the books indicated, but hang down below the leaves on slender recurved pedicels. In the summer of 1938, in the same neighborhood, I looked into the matter further, collected some more specimens, also examined the seeds for the first time.

I found the seeds to be about 10–12 mm. long and nearly as wide, broadly winged, chestnut-colored, and entirely devoid of the long apical hairs which in other species of *Asclepias* function like a parachute for dispersal by wind. And instead of lying parallel to the walls of the pod, hanging downward from its apex (which is uppermost in most species), and overlapping like shingles, as in all the well-known species of the genus, they were attached to a narrow longitudinal placenta by one end, and lay almost at right angles to the length of the pod, closely piled like a stack of coins.

The specimens illustrated herewith were collected on Sept. 7, 1938 (no. 3697) in and around a tupelo gum (*Nyssa uniflora*) slough (called "Goose Pond" on the recent government topographic maps) in the alluvial bottoms of the Warrior River, about six miles west-southwest of Tuscaloosa. On account of the dense shade and lack of a contrasting background it was impractical to photograph them on the spot, but they were photographed in my office a few hours later, before the leaves had wilted perceptibly, and then pressed.

A skeptic inclined to accept as gospel the statements in the books about "follicles erect on erect pedicels" might imagine that the pedicels in the specimens photographed had drooped with partial wilting, or been bent down purposely. But it should be evident enough from the photograph that the pedicels are too long and slender to hold a fruit of that size erect.[2] At the time of collection some of the follicles were still green and unopened, and some in various stages of dehiscence. Some of the ripe seeds were scattered beside the plants when photographed, to show their size, which is probably the largest in the genus.

The other illustration shows the vegetation in Goose Pond, with *Nyssa uniflora* predominating, as it appeared on July 30, when the water may have been two feet deep in the center. The *Asclepias* did not grow in the deepest parts, but chiefly about where the edge of the water was at that time, and also a little farther away. At the time the specimens were

[2] I have not had access to a large herbarium recently, but Charles C. Deam of Bluffton, Ind., the best living authority on Indiana plants, showed me a fruiting specimen of *A. perennis* from the Wabash bottoms of southwestern Indiana when I visited him in the fall of 1938, and a few days later he got another for me from the same neighborhood; and these plants are scarcely distinguishable from my Alabama specimens.

collected, nearly six weeks later, the water had practically disappeared, but the middle of the slough was still pretty muddy.

Throughout the range of *Asclepias perennis* the streams are generally highest in winter and spring, when the plants are dormant. When they bloom in summer the water is usually receding, and probably in most years when the seeds are ripe the ground under the plants is bare. If such a plant grew on a prairie and held its follicles erect the broadly winged seeds might be carried a few yards by the wind, but there can be little wind in the depth of the swamps, and (figuratively speaking) the plant evidently does not count on any such assistance. So it hangs its follicles down, and when the seeds are discharged they must fall to the ground, to lie until the winter and spring rains raise the water again and float them away.

It has been said by some good authority[3] that different modes of dissemination seldom occur in the same genus. I am not at present proposing to establish a new genus for *Asclepias perennis* on account of its seed without coma (and a few other peculiarities that have been mentioned), but it would seem to deserve that status better than some other recent segregations from the genus, and it should probably be set off in a section by itself, as Chapman had it, instead of being grouped with species that are very unlike it. But we need to know more about the little-known *A. texana*, which may be a connecting link.

In mode of dissemination there is an interesting analogy between *Asclepias perennis* and *Quercus lyrata* (also first described by Walter), which has a similar range and habitat, and can often be found in close proximity to the *Asclepias*. The acorns of that oak have a corky layer around the seed, which together with the enclosing cup enables them to float; and that species may be the only oak in the world with floating acorns.[4]

A character that applies to the whole genus *Asclepias*, and some if not most of the other genera in the same family, but is seldom if ever mentioned in the books, should be noted here. In the whole family, as in the allied Apocynaceae, the gynoecium consists of two carpels. In the Apocynaceae both carpels usually develop, into a pair of slender follicles, but in *Asclepias* it is very exceptional for more than one from a single flower to mature. Not only that, but of all the numerous flowers in each umbel, all apparently perfect and with equal opportunities for pollination, it is

[3] I do not now recall where I first read this, but I referred to it in Torreya 8: 159, 160. 1908.

[4] I discussed this at the St. Louis meetings of the Ecological Society of America in December, 1935, and exhibited there cross-sections and photographs of the acorns, but have published nothing on it as yet but a brief note in the program for that meeting.

unusual for more than one to produce any fruit; just as if in a large family only one of the children married.

When the seed of any of the common species of *Asclepias* goes floating off through the air, the silky hairs that form a tuft at its apex look very much like the pappus on the achenes of many Compositae, which is a modified calyx-limb. But the coma in *Asclepias* is of course very different morphologically. These hairs are not mere trichomes either; for in the ovary they are the means of attachment of the seed to the placenta, and the pollen tubes must find their way to the ovules through them; a fact not mentioned in any description that I have seen.

The fruits of some other genera of Asclepiadaceae have been inadequately described, probably for the same reason as in *Asclepias perennis,* namely, they are seldom collected.

In 1818 Thomas Nuttall described the genus *Enslenia,* with a single species, *E. albida,* a twining vine growing on river banks in Virginia and Ohio. Although it is now known as far south as Georgia, if not Florida, Elliott was not acquainted with it, and it is not mentioned in the first edition of Chapman's Southern Flora, 1860. Chapman described it in the supplement which was added to the first edition to make the second edition, in 1883, and said of the fruit only "follicle fusiform."

Britton in 1894[5] discovered that Nuttall's *Enslenia* was antedated by an *Enslenia* of Rafinesque, 1817, but found another generic name of Rafinesque's, *Ampelamus,* that applied to our vine, and transferred the species to that. As *Ampelanus albidus* it is described and figured in the first edition of Britton and Brown's Illustrated Flora (3: 16. 1898). The illustration shows a smooth follicle with the apex upward, and the description says "follicles erect on the ascending fruiting pedicels, 4′–6′ [inches] long, glabrous when mature."

The following year Miss Anna M. Vail,[6] after a study of type specimens in Paris, announced that Michaux's *Gonolobus laevis* (1803), from Illinois, was the same as Nuttall's *Enslenia albida;* and accordingly Michaux's name, which was 15 years older than Nuttall's, has been used by subsequent American writers. She mentioned that the follicles in the type specimens were angled; and that was accepted as typical of *Enslenia* (*Ampelanus*) by Small, who in his description of "*Gonolobus laevis*" (Fl. S.E. U.S., 951–952) in 1903 said: "follicles erect on spreading pedicels, 10–15 cm. long, glabrous, wing-angled." Robinson and Fernald in 1908 said of the same plant: "follicles elongate-ovoid to lanceolate,

[5] Bull. Torrey Bot. Club 21: 314. 1894.
[6] Bull. Torrey Bot. Club 26: 427. 1899.

smooth," but nothing about angles—except inferentially in translating the generic name *Gonolobus*—or about the size or position of the fruit. Small's Manual, 1933, repeats the statement "follicles wing-angled," but his illustration shows no wings.

Miss Lily M. Perry has recently thrown a little new light on the subject.[7] Miss Vail in her study of 1899 noted that the supposed type of Michaux's *Gonolobus laevis* consisted mostly of numerous small pieces, "but all of the specimens in the two collections agree and point unmistakably to the plant since called *Enslenia albida* Nutt." A little farther on, however, she admitted the presence of a fragment of *Gonolobus suberosus* (*Vincetoxicum suberosum* (L.) Britton) on one of the sheets. Miss Perry pointed out that the flowers of the type specimen do not agree at all with Michaux's generic description of *Gonolobus*, and that Dr. Gray had interpreted it quite differently from Miss Vail. But she made no special comment on the fruit, apparently being willing to let that go as representing *Enslenia*.

Dr. Charles Mohr, reporting on this species in his Plant Life of Alabama,[8] knew it only from a specimen collected in Jackson County, in the Tennessee Valley, by some anonymous collector for the Biltmore Herbarium. But in the fall of 1908, having previously become acquainted with it in Georgia, I saw what I took to be it at a few places along the Tombigbee River in southern Alabama. I noted then that, contrary to current descriptions, the juice of the plant was not milky, and its follicles were neither angled nor erect; and on account of these discrepancies I was not sure that I had identified it correctly.[9]

I did not see the fruit of *Enslenia* ("*Gonolobus*") again until September, 1938, when I found the vine climbing over a hedge in the yard of a friend in the outskirts of Lexington, Kentucky. There I verified my observation of nearly thirty years before, that the pods were not at all angled (though a little wrinkled longitudinally), and they hung down, as such heavy objects would necessarily have to do on a slender herbaceous vine, no matter how stout their pedicels. An exception to this, however, was afforded in occasional instances where both follicles from the same flower developed. In such cases they diverged at an angle of 180,° and would probably have been horizontal if one had not been a little larger than the other, upsetting the balance.

[7] Rhodora **40**: 281–283. 1938.

[8] Contr. U. S. Nat. Herb. **6**: 677. 1901.

[9] Bull. Torrey Bot. Club **37**: 115. 1910.

It would appear from the writings of Miss Vail and Miss Perry, already cited, that the specimens labeled *Gonolobus laevis* by Michaux include flowers of *Enslenia* (*Ampelamus*) and follicles of another twining genus of the same family, with very different flowers and fruit, which was described as *Vincetoxicum*[10] by Walter in 1788; and this has led several writers since Miss Vail to the belief that the follicles of *Enslenia* are angled. Of course it is barely possible that Michaux really had a species of *Enslenia* with angled follicles, different from the more southerly one; but his genus *Gonolobus* when published included two other species, which are considered typical *Vincetoxicums*, and the *Enslenia* flowers may have been mounted on the sheet of *G. laevis* by some careless person after his death, for he died before his Flora Boreali-Americana was published, and the work was completed by L. C. Richard. In any case, the name *Gonolobus*, which means angle-pod, cannot be considered as typified by the species under discussion, whose pods are not angled.

Although the usual habitat of our plant is river-banks, and it does not seem hitherto to have been charged with weedy tendencies, it was certainly a weed at the Kentucky station above mentioned, and many miles from any river. And in the last few years I have found it climbing on cultivated shrubs on the campus of the University of Alabama. That is about half a mile from the Warrior River, but I have not yet observed it along that river. I collected a flowering specimen (no. 3588) on the campus on July 22, 1937, but ever since I have known the station the vines have been torn out by gardeners before they had a chance to make fruit.

University, Alabama

10 The application of this name, which does not particularly concern us here, was discussed by Miss Perry in the paper cited. Several species with follicles muricate as in *Asclepias Syriaca,* instead of angled, were put in a separate genus, *Odontostephana,* by E. J. Alexander in Small's Manual, 1933, but those are put back in *Gonolobus* without explanation by Miss Perry.

A New Species of Tetraëdron from Minnesota

CHARLES B. REIF

(WITH TEN FIGURES)

Tetraëdron grande sp. nov.

Cellulae singulae pelagicae 4–angulatae forma tetrahedrica ad unum planum angulis productis in spinas longas solidas pariete convexo 4μ crasso. Longitudo cum spinis 135μ; latitudo cum spinis 87μ.

Cells four angled, basic four-sided shape tending toward one plane with two sides, the angles produced into long, tapering, solid spines; these spines occasionally undulating at tip but never furcate or decorated; cells solitary free floating and pelagic; walls smooth, 4μ thick; wall bearing lateral spines more convex than wall of long axis.

This species is much larger than any heretofore described in the genus Tetraëdron. Measurements of forty individuals gave the following averages($\bar{x}$). The dimensions taken are indicated on figure ten and all are expressed in microns.

Dimension	*A*	*B*	*C*	*D*	*Thickness*
$\bar{x}$	134.9	67.8	87.1	49.8	37.7
s_x	9.9	5.5	9.8	3.9	3.2

This species is placed in Section I, Polydrium (Naegeli) Hansgirg of the genus Tetraëdron. It is most closely related to *T. quadricuspidatum* (Reinsch) Hansgirg which approaches the new species both in size and form. The separation of the two species is made on the difference of twenty microns in size and the positions of the lateral spines. In *T. quadricuspidatum* the lateral spines tend to curve more toward one end, forming a trident shape, whereas in the new species the lateral spines are more independent and may even project almost at right angles to the long axis. Both of the above species are related to *T. regulare* Kützing. *T. tortum* West is nearly equal in size but there can be no confusion between its twisted shape and the graceful lines of the species here described.

Tetraëdron grande has been found in four eutrophic lakes of west-central Minnesota. All of these lakes are of the same character and lake type as shown by the following physical data (Table 1) taken at the same time the plankton collections were made in which the alga appeared.

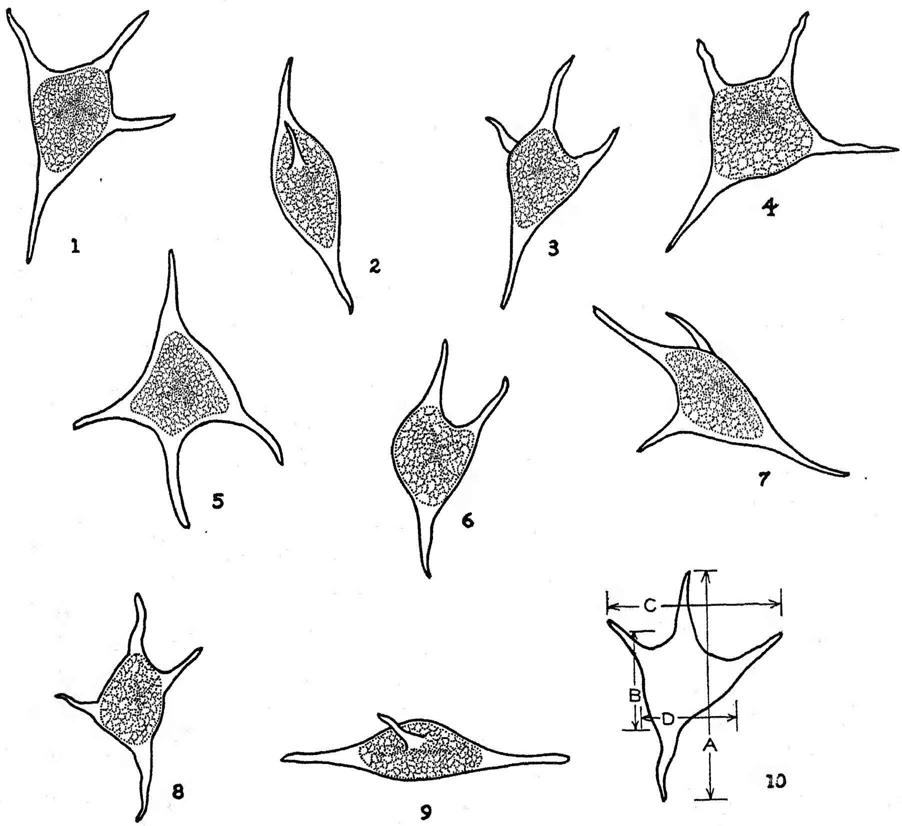
It will be noted that the records fall in the months of August and September. Samples taken from these lakes in June contained no individuals of this species. In all four lakes the most common plankter on the dates given above was *Ceratium hirundinella*. Another interesting

TABLE 1

Physical Characteristics of Lakes

Lake	*Date*	*pH*	*—HCO_3*	*Tot. dis. solids*	*Temp.*
GILSTEAD	8/22/36	8.2	160 ppm.	250 ppm.	70° F.
NORTH STAR	8/10/36	8.4	102 ppm.	173 ppm.	72° F.
BALL CLUB	9/ 2/36	8.2	131 ppm.	124 ppm.	65° F.
OTTERTAIL	9/13/36	8.4	231 ppm.	647 ppm.	68° F.

association which was present in all of the four cases cited was that of *Coelosphaerium Kützingianum*, *C. Naegelianum* and *Melosira granulata*. These three species were predominant in the order named.



Figs. 1–10. Various aspects of *Tetraëdron grande* sp. nov. × approx. 275.

Vertical samples indicated that in Gilstead lake *Tetraëdron grande* occurred slightly more abundantly at the four metre level than at the surface, although it was present at the eight and twelve metre levels as well. This has been shown to be a normal distribution for most Chlorophyceae.

UNIVERSITY OF MINNESOTA

New and Unusual Species of Uredinales[1]

E. B. Mains

In this paper, data are presented concerning a number of species of rusts based on information obtained from collections which have been received from time to time from various sources. All specimens, including types, have been deposited in the Herbarium of the University of Michigan.

Coleosporium Madiae Cooke

In 1937, a collection of a rust on *Argyroxiphium sandwicense* DC. was received from Willis W. Wagner of the Division of Forestry of the United States Department of Agriculture. The collection was made by Eric Walther in the rare plant garden of the Golden Gate Park, San Francisco, California. The host is a Hawaiian species for which no rust has been reported. The rust proves to be *Coleosporium Madiae* which occurs on various species of *Madia* on the Pacific coast of the United States. *Argyroxiphium* and *Madia* are closely related genera of the *Heliantheae* of the *Compositae.* If *Coleosporium Madiae* should be introduced into Hawaii it doubtless would become an important parasite of *Argyroxiphium.*

It is interesting to note that M. W. Gardner has recently reported *C. Madiae* on African Marigold at San Juan, California. The host, *Tagetes erecta,* is also an introduced species for which the rust had not been previously reported.

Puccinia Ammophilina comb. nov.

Uredo Ammophilina Kleb. Krypt. Flora Mark Brandenburg 5A: 882. 1914.

Uredinia epiphyllous, between the veins, cinnamon-brown, ruptured epidermis evident; urediniospores broadly ellipsoid, 22–26$\times$26–36μ, the wall yellowish or brownish 1.5–2.5μ, moderately echinulate, the pores 6–8 scattered; paraphyses variable in abundance, capitate, up to 60μ long, 6μ wide below, the head 12–20μ, the wall hyaline, 1μ.

Telia epiphyllous, between the veins, chestnut- to chocolate-brown, somewhat tardily naked, the ruptured epidermis evident; teliospores clavate to oblong-clavate, 16–22$\times$38–62μ, the wall yellowish-brown below, chestnut-brown above, 1μ thick below, 4–5μ at the apex, the pedicel short, fragile.

On *Ammophila arenaria* (L.) Link, Lake Lytle, Oregon, Nov. 4, 1936 (Ore. no. 10–733); Lake Lytle, Oregon, March 8, 1938; Twin Rocks,

[1]Paper from the Department of Botany and the Herbarium of the University of Michigan.

Oregon, Sept. 24, 1937, R. Sprague; *A. breviligulata* Fernald, on sand dunes, AuTrain, Michigan, Aug. 24, 1932, E. B. Mains (32–285).

Rust on *Ammophila arenaria* and *A. breviligulata*, two very closely related species, has apparently not previously been reported from North America. In Europe, two species, *Uredo Ammophilae* Syd. and *U. Ammophilina* Kleb. have been known. *Uredo Ammophilae* is described as having urediniospores 21–26μ or 18–24 x 26–34μ with walls 2–3μ thick. It lacks paraphyses. *Uredo Ammophilina* differs in having capitate thin-walled paraphyses and urediniospores 21–26 x 27–39μ and walls 1.5μ thick. The North American collections agree well with the latter. The occurrence of teliospores in the Oregon collections received from R. Sprague makes it possible to place this species in Puccinia.

Puccinia amphigena Diet.

A collection of rust on *Ammophila breviligulata* Fernald, made by G. W. Martin (1650) at Mineral Springs, Indiana, Sept. 23, 1931, was received from G. B. Cummins. This has abundant amphigenous telia, containing some urediniospores. The collection appears to be *Puccinia amphigena* which has previously been reported only on species of *Calamovilfa*. A comparison of the descriptions of the uredinia of *P. amphigena* and *Uredo Ammophilae* shows a very close similarity and suggests that they may be the same species. Opposing this is the scanty and amphigenous development of uredinia of *P. amphigena* and the abundant epiphyllous development of uredinia of *U. Ammophilae*.

Frommea mexicana sp. nov.

Urediniis hyophyllis, sparsis, mox nudis, pulverulentis, pallide flavis; urediniosporis ellipsoideis vel obovoideis, 13–16$\times$16–20μ, membranis tenuissimis, 0.5μ, hyalinis, echinulatis, poris inconspicuis; teliis hypophyllis, sparsis, subpulverulentis, cinnamoneo-brunneis; teliosporis cylindriceo-clavatis, 23–32$\times$38–60μ, apice rotundatis, basi rotundatis vel vix attenuatis, 2–3–septatis, membranis 1.5–2μ crassis, apice 4–6μ, pedicellis usque 50μ longis, hyalinis.—*Fragaria mexicana* Cham. and Schlect. Chapulhuacan, Hidalgo, Mexico VII. 12, 1937, C. L. et Amelia Lundell (7182, specimen typicum).

The Sydows (Monograph. Ured. 3: 102. 1915) doubtfully list *Fragaria vesca* as a host of *Phragmidium Fragariastri* in Europe. Otherwise this is apparently the first record of a rust on a strawberry. *Duchesnea indica*, the host of *Frommea Duchesneae* at one time was placed in Fragaria but is now generally recognized as generically distinct. It

supposedly was introduced from Asia yet the rust is known only from North America. This suggests that the rust originally occurred on an indigenous host and Fragaria would be a logical source. Opposing this, however, is the absence of rust on Fragaria in the area where *Frommea Duchesneae* occurs.

The species of *Frommea* are very closely related. *Frommea obtusa* (Str.) Arth. is widely distributed in the temperate portions of the northern hemisphere on species of *Potentilla*. *Frommea Duchesneae* Arth. occurs in the southeastern United States on *Duchesnea indica*. The teliospores of *F. obtusa* are 2–6–septate and measure 20–27 x 40–90μ and the urediniospores are 15–20 x 19–26μ with walls 1.5–2μ thick. The teliospores of *F. Duchesneae* are 2–4–septate and measure 19–26 x 50–80μ and the urediniospores are 12–17 x 15–21μ with walls 1μ thick.

Puccinia cornuta Jacks. & Holw.

On *Notoptera scabridula* Blake, Cohune Ridge, El Cayo, British Honduras, July 11, 1936, E. B. Mains (3798). Only pycnia and aecia occur in this collection. It differs somewhat from the description of the species. The aecia are lighter in color and the aeciospores more irregular, often having 2 or 3 rather prominent projections. Arthur (Am. Jour. Bot. 5: 533. 1918) reported the species from Guatemala on *Notoptera brevipes* (Robinson) Blake.

Puccinia Ichnanthi sp. nov.

Urediniis amphigenis, sparsis, cinnamoneis, 0.2–0.5 mm. dia.; urediniosporis late obovoideis vel ellipsoideis, 22–30$\times$30–44μ, membranis cinnamoneis, 1.5–2.0μ crassis, conspicue echinulatis, poris 2–3, aequatorialibus; teliis hypophyllis, pallide brunneis, 0.2–0.5 mm. dia.; teliosporis fusoideis, 12–14$\times$28–34μ, membranis hyalinis vel pallide brunneis, tenuissimis, 1μ, pedicellis hyalinis, 12–30μ longis.—*Ichnanthus candicans,* (Nees) Doell, Tijuca, Dist. Federal, Brazil, IV. 28, 1930, Agnes Chase (12143A, specimen typicum).

This rust was obtained from a phanerogamic specimen in the Herbarium of the University of Michigan. The urediniospores are very similar to those of *Puccinia inclita* Arth. which has been reported on species of *Ichnanthus*. The teliospores are very different and unusual for a grass rust. They have colorless or brownish, very thin walls which are uniform in thickness. They germinate at once. In these characters the rust agrees with species which have been placed in the genus *Eriosporangium*. However, the species of *Eriosporangium*, for which the full life-cycle is known,

all have been autoecious and the aecia in most species have lacked perida. Most species of grass rusts have been heteroecious and the aecia have well developed peridia. Except for species of *Angiopsora* the grass rusts have been either species of *Puccinia* or *Uromyces* and it seems best for the present, at least, to place this species in *Puccinia*.

Puccinia Nephrophyllidii sp. nov.

Urediniis amphigeniis, hypophyllis, sparsis, 0.2–0.5 mm. dia. tarde nudis, pulverulentis, cinnamoneo-brunneis; urediniosporis late ellipsoideis, 22–26$\times$28–32μ, membranis cinnamoneo-brunneis, 2–2.5μ crassis, moderate echinulatis, poris 1–3, semper fere 2, superaequatorialibus; teliis amphigenis, hypophyllis, sparsis, 0.5–0.8 mm. dia., tarde nudis, pulverulentis, atri-brunneis; teliosporis variabilis, irregulater oblongis, ellipsoideis vel clavatis, 20–32$\times$36–68μ, membranis castaneo-brunneis, 2–2.5μ crassis, ad apicem papillula 6–7μ alta, instructis, pedicellis hyalinis, brevis.—*Nephrophyllidium Crista-galli* (Meng.) Gilg, Ketchikan, Alaska, VIII. 3, 1938. D. V. Baxter.

The host belongs in the *Gentianaceae* and has been included by some botanists in the genus *Menyanthes*. Apparently no rust has previously been reported for either *Nephrophyllidium* or *Menyanthes* and the species is distinct from other rusts of the *Gentianaceae*.

Puccinia ripulae nom. nov.

Puccinia riparia Mains, Papers Mich. Acad. Sci. Arts and Letters 22: 156–157. 1937. non *Puccinia riparia* Holway, Jour. Mycology 10: 163. 1904.

In 1937, a rust collected on *Baccharis glutinosa* at Alamo, Hidalgo Co., Texas by Elzada N. Clover (1130) was described and named *Puccinia riparia*. Dr. Grant D. Darker has called my attention to the fact that the name *P. riparia* was previously applied to a rust of Carex by Holway. Arthur (North Am. Flora 7: 355. 1920) has considered this a synonym of *Dicaeoma Grossulariae* (Schum.) Kern [= *Puccinia Caricis* (Schum.) Scroet.]. It is therefore necessary to give a new name to the rust of *Baccharis* and *Puccinia ripulae* is proposed.

Pucciniastrum alaskanum sp. nov.

Urediniis hypophyllis, subepidermalibus, sparsis, 0.2–0.3 mm. dia. poro centrali apertis; peridiis hemisphaericis, ex cellulis minutis compositis; urediniosporis oblongis vel anguste ellipsoideis, 12–16$\times$24–40μ, membranis hyalinis, 1.5μ crassis, minute echinulatis, poris inconspicuis; teliis ignotis.—*Gentiana glauca* Pall., Mt. McKinley National Park, Alaska, VII. 19, 1933, D. V. Baxter.

Although telia have not been seen, the uredinia are characteristic for *Pucciniastrum*. *Pucciniastrum Gentianae* as described by Hiratsuka and Hashioka (Tottori Soc. Agr. Sci. 5: 237. 1935) from *Gentiana formosana* in Japan has shorter and broader urediniospores (17–23 x 21–27μ) and thicker urediniospore-walls (2–3μ).

Uredo detenta sp. nov.

Urediniis hypophyllis, sparsis, 0.5 mm. longis; urediniosporis late ellipsoideis vel obovoideis, 20–28$\times$28–36μ, membranis atri-cinnamoneis, 2.5–4μ crassis, conspicue echinulatis, poris 3–4, equatorialibus.—*Olyra micrantha* H. B. K. Gavea, Estado do Rio de Janeiro, Brazil, Nov. 2, 1929, Agnes Chase (9981A, specimen typicum); Avenida Niemeya, Rio de Janeiro, Nov. 5, 1929, Agnes Chase.

This rust was obtained from phanerogamic specimens in the Herbarium of the University of Michigan. The urediniospores of this species are smaller than those of *Puccinia belizensis* Mains described (Contrib. Univ. Mich. Herb. no. 1, p. 8. 1939) from *Olyra latifolia* from British Honduras.

University Herbarium
University of Michigan
Ann Arbor, Michigan

A New Species of Cuscuta from Yucatan

T. G. Yuncker

(WITH ONE FIGURE)

Cuscuta palustris sp. nov. Caules crassitudine modici usque tenues. Flores subcarnosi, 5– aut 4–divisi, circ. 2 mm. longi a basi ad corollae sinum. Pedicelli floribus, aequilongi vel breviores. Inflorescentia paniculato-cymosae. Calycis lobi ovato-lanceolati, acutissimi, ad basin plus minusve imbricati, sinibus obtusis. Corollae lobi acutissimi, ovato-lanceolati, tubo campanulato aequilongi vel

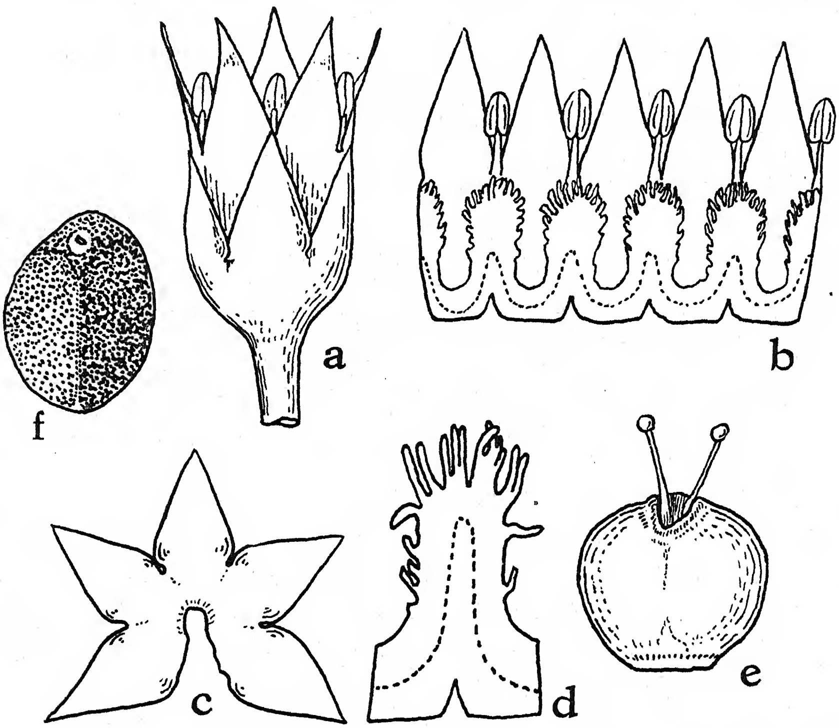


Fig. 1. *Cuscuta palustris* Yuncker, n. sp. a, flower ×*10;* b. opened corolla ×*10;* c, opened calyx ×*10;* d, individual scale ×*20;* e, capsule ×*10;* f, seed ×*20.*

plerumque longiores. Filamenta subulata; antherae ovato-longae. Squamae oblongae, fimbriatae, stamina attingentes. Styli plus minusve subulati, ovario globoso aequilongi vel breviores. Capsula depresso-globosa, membranacea, non circumscissilis. Semina 4, circ. 1.5 mm. longa, hilo brevi oblongo.

Stems moderate to slender. Flowers somewhat fleshy, 5– or sometimes 4–parted, about 2 mm. long from the base to the corolla sinuses or 3 to 4 mm. long to the tips of the erect corolla lobes, on pedicels about equaling the length of the flowers, in paniculate-cymose clusters. Calyx more membranous than

the corolla and yellow when dry, lobes somewhat thickened medianally, longer than the corolla tube, ovate-lanceolate, sharply acute, overlapping but abruptly narrowed at the base to form an obtusely rounded sinus, margins essentially entire. Corolla somewhat fleshy, campanulate, enlarging and remaining about the base of the mature capsule, lobes at first erect but becoming reflexed as the fruit develops, equaling or mostly longer than the tube, ovate-lanceolate, sharply acute, abruptly narrowed at the base, margins entire or some lobes sparingly irregular. Anthers ovate-oblong, about as long as the stoutish, subulate filaments. Scales reaching the stamens, oblong, fringed with medium length processes, bridged below the middle. Styles more or less subulate, stoutish, about equal to or slightly shorter than the globose ovary, stigmas depressed-globose. Capsules depressed-globose, membranous 4–seeded, thin about the base and easily breaking loose from the calyx but they do not appear to be definitely circumscissile, interstylar aperature gaping. Seeds about 1.5 mm. long, oval in outline, umbilical area round, hilum short, oblique, embryo filiform, coiled.

MEXICO: Progresso, Yucatan, in salt marsh, August 11–15, 1932, W. C. Steere *no. 3077*. (Type in herb. Univ. Michigan).

The type specimen is not abundant or in very good condition. A sufficient number of flowers and fruits are present, however, to show that it does not agree with any other known species. It apparently belongs in subsection Acutae of section Cleistogrammica and seems to be most closely allied with *C. acuta* Englm. of the Galapagos islands and *C. yucatana* Yuncker. It differs from both of these species with its mostly larger and somewhat fleshier flowers, more lanceolate perinth lobes which are abruptly narrowed at the base, and with stouter filaments and larger anthers.

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Two Pocket Rots of Hardwood Trees

W. H. Long

(with four figures)

This paper describes a butt heart-rot of living trees caused by *Fomes extensus* Lev. and a honey-comb rot of dead fallen timber produced by *Polyporus rigidus* Mont.

During field investigations in Florida (1913-1918), the writer found the hymenophores of *Fomes extensus* associated with a white pocket heart-rot of three species of living trees—*Exothea paniculata* (Juss.) Radlk., *Lysiloma bahamensis* Benth. and *Taxodium distichum* (L.) L. C. Rich. This rot was always in the base of the infected trees, extending downward into the roots and also upward in the butts for a short distance (2–3 ft.).

In *Exothea paniculata*, the first indication of the rot is a slight change in the color of the heartwood, small whitish flecks appear which later increase in size. The white color is due to the delignification of the wood by the fungus leaving the cellulose intact. In early stages of the rot, the white pockets are lense-shaped and in radial section range from 2–10 mm. wide by 5–20 mm. long with their main axes parallel to the grain of the wood. These pockets are filled with white cellulose which is slowly absorbed by the attacking fungus leaving small cavities lined with the remnants of the cellulose fibers. These white pockets increase in size faster longitudinally than radially. The cross walls of the pockets, which originally ran radially are gradually destroyed by the fungus thereby causing the rotting wood to separate into thin longitudinal irregular sheets whose central layer consists of dark brown partially rotted wood.

The pockets produced in this host are very pronounced and in the last stages of the rot much, but not all, of the attacked heartwood is destroyed, leaving big pockets lined with white cellulose fibers. In the oldest stages of the rot the partially empty pockets may have a light, fluffy mass of mycelium in their centers.

Figure 1 gives a cross-section view of an advanced stage of the rot in the heartwood of *Exothea paniculata;* figure 2 shows a radical-longisectional view of the rot in the same host. The description and photographs were made from specimens of the rot in the living exposed roots found near Miami, Florida.

Fomes extensus causes a rot in the heartwood of *Lysiloma bahamensis* very similar to that in *E. paniculata,* however the rot pockets are smaller in cross-section view but have the same tendency to coalesce longitudinally

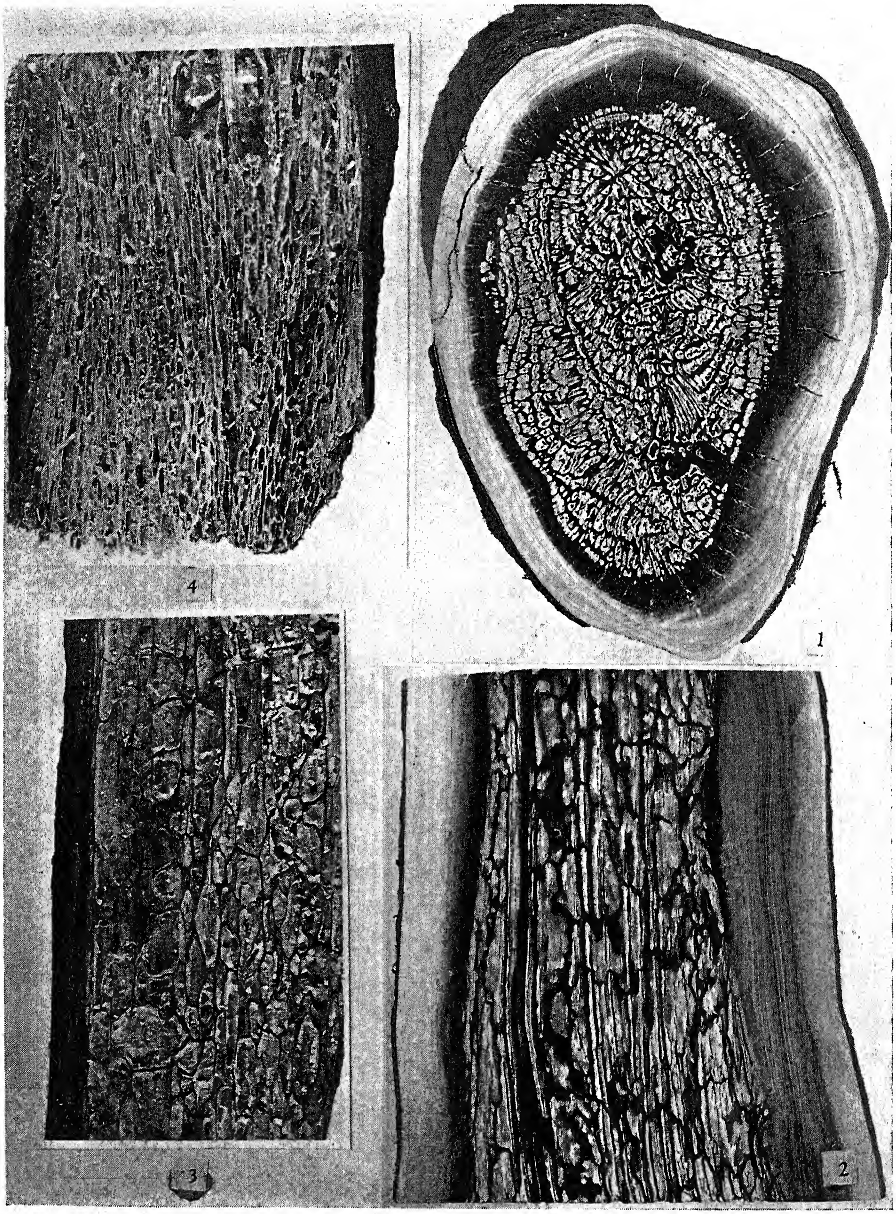

Fig. 1. *Fomes extensus* rot in roots of *Exothea paniculata*, Miami, Fla. Cross-section view. ×¾.

Fig. 2. *Fomes extensus* rot in roots of *Exothea paniculata*, Miami, Fla. Radial-longisection view. ×¾.

Fig. 3. *Polyporus rigidus* rot in *Liquidamber styraciflua* long Lake Village, Ark. Radial-longisection view. ×1.

Fig. 4. *Polyporus rigidus* rot in *Liquidamber styraciflua* log, Cass, Ark. Tangential-longisection view. ×1.

thereby producing a continuous line of delignified rot. With age many of these pockets are filled with a brown mycelium. This description was made from specimens of the rot in *L. bahamensis* collected near Miami, Florida.

F. extensus was also found associated with a heart-rot in the butts of living trees of *Taxodium distichum.* The rot pockets in this host are much larger than those in the other two hosts given above. These pockets ranged from 1–2 cm. wide by 4–8 cm. long. Only a trace of the cellulose fibers were left in the specimens at hand. The pockets were empty except for a thin whitish arachnoid mycelial membrane on the walls. The partitions separating the pockets were very thin (0.5–1 mm. thick). This description was made from specimens of the rot found near Palatka, Florida, in the butt of a living tree, directly associated with a hymenophore of *Fomes extensus.*

While investigating forest tree diseases in the Mississippi River Valley (1913–1918), the hymenophores of *Polyporus rigidus* were found associated with a characteristic honey-comb rot in the logs and stumps of *Liquidamber Styraciflua* L. This fungus was also found attacking the dead fallen trees of *Nyssa aquatica* Marsh, *Platanus occidentalis* L. and *Quercus alba* L., but the rot found in these three species was not as pronounced a pocket rot as that in *L. Styraciflua.*

The rot pockets produced by *P. rigidus* in *L. Styraciflua* are lenticular and in the last stages are filled with a white arachnoid mycelium. In radial-longisection these pockets are broad and are bounded by the medullary rays of the wood. They are longer than broad, being 0.5–1 cm. broad by 1–2 cm. long (fig. 3). In tangential-longisection these pockets have a very different appearance, being 0.2–0.5 cm. thick by 1–2 cm. long (fig. 4). In the final stages of this rot the infected wood becomes very light and of a honey-comb consistency. No early stages of the rot were seen. This fungus was found in Arkansas, Mississippi, Tennessee, Texas and Virginia.

Dr. L. O. Overholts, who kindly identified my material of *Polyporus rigidus,* states in a recent letter, that he has also found *P. rigidus* producing a conspicuous pocket rot in the south and that it is very similar to the rot caused by *Polyporus zonalis* Berk. in the same region. He says that *P. rigidus and P. zonalis* are closely related, having the same minute thick-walled tubes, similar spores, hyphae and basidia and in the peculiarly hardened condition of the dried specimens of each.

Polyporus rigidus is usually resupinate but occasionally develops a very narrow reflexed pileus. The resupinate material has been identified by some American and European botanists as *Poria undata* (Pers.) Bres.

ALBUQUERQUE, NEW MEXICO

A New Forest Climax: the Salt Spray Climax of Smith Island, N. C.

B. W. Wells

(WITH TWO FIGURES)

Smith Island, N. C. (locally called Bald Head Island) has always been of unusual interest to botanists because of the high dominance of live oak on its upland areas together with the fact that the cabbage palmetto reaches its most northerly limit here.

A glance at a map of the eastern shore line of the United States will show that the tip of Cape Fear is on this island and the island bounds the eastern side of the mouth of Cape Fear River. It is made up of a series of 3 narrow sand uplands alternating with 2 salt-marsh lowland areas and extensive salt marshes to the north (fig. 1). The long axes of these physiographic structures are approximately east-west. By far the largest of these land strips is the most southerly one which, according to the latest hydrographic map (Geodetic Survey), is 3 miles long and ½ mile wide at the eastern end, but a mile wide at the western end.

The inland two-thirds of this "main island" is covered with a unique forest of live oak (*Quercus virginiana*)—unique in the sense that this tree here forms a practically pure stand with crowns meeting (fig. 2), except for an occasional palmetto (Sabal palmetto) holding its mass of fan-like leaves 20–30 feet in the air. Earlier there was a second important tree, through not to be regarded as subdominant; viz., the red cedar (*Junipus virginiana*). This tree was cut extensively in the past leaving the oak to assume an unusually high degree of dominance. These oaks today give every evidence of being climax. Very old living trees with trunk diameters of 3–4 feet are frequent, and scattered in them one encounters disintegrating trunks of even larger trees. In addition to this direct evidence, a report on the Island made in 1805 by J. G. Swift, an officer in the U. S. Army, states concerning the mouth of the Cape Fear River; "On Smith Island there is a growth of live oak and palmetto." There can thus be no question of the climax status of this forest.

The topography of the forested area is of a low rolling type, the local elevations 5–10 feet high representing small dune relics. The live oaks occupy the low flat areas as well as the dune summits. The soil is sufficiently high in humus to give it a loam structure. The high degree of maturity reached is reflected in the frequency with which the flowering dogwood is present under the canopy of live oaks. Under the rainfall (average of 50

inches recorded at nearby Southport) this soil may be regarded as definitely mesic and favorable for the growth of the ordinary broad-leaved climax species of the region; viz., white, black, and southern red oaks or even beech and southern sugar maple.

Yet these trees are wholly absent and the accompanying undergrowth is largely made up of the shrubs *Batodendron arboreum*, *Myrica cerifera*, *Ilex vomitoria*, *Osmanthus americanus*, *Callicarpa americana*, and the small trees, *Persea borbonia*, *Prunus lauro-cerasus* and *Ilex opaca*.

On the mainland, and back a mile or more from the sea, in sharp contrast to the Island, the live oak nowhere assumes dominance, or subdominance. In North Carolina it disappears almost completely a few miles from the sea if the numerous transplants to private grounds are ignored.

Mohr (1) has earlier pointed out that "*Quercus virginiana* is a tree of the sea coast. It approaches in a high state of development the Carolinian area near the northern limit of eastern North Carolina and extends westward along the Gulf coast to Texas and northern Mexico. In the Gulf states the live oak is rarely found above the 31st parallel."

It is the purpose of this paper to explain this local dominance of *Quercus virginiana* along our eastern and southern coast and to show that this tree when it reaches high dominance and stabilization constitutes a new and heretofore unrecognized kind of climax.

Wells and Shunk (2) working on the coastal vegetation of the Cape Fear Peninsula discovered that the characteristic sloping forms of the woody plants nearest the sea, which had heretofore always been ascribed to wind, are not directly due to wind but are produced by the killing or blighting action of the salt water spray carried by the wind. Full proof of this assertion was found in the numerous examples of the same coastal woody plants which occupied sites fully exposed to the wind but far enough back from the sea to remove them from the spray zone. Such shrubs and trees showed no detectable modification of their contours.

In making these original observations it was quickly noted that the live oak was the only dicotyledonous tree (*Myrica cerifera* and *Ilex vomitoria* are seen chiefly as shrubs) which can tolerate the medium spray intensity or occupy the middle spray zone sites. It is not as resistant to the spray injury as the two shrubs just mentioned. Correlated with the relatively high spray resistance of live oak are the structural characteristics of its sclerophyll leaf, with its thick cutin and absence of stomata above, and the closely spaced myriads of stellate trichomes below preventing any ready access of water to the stomatal bearing surface.

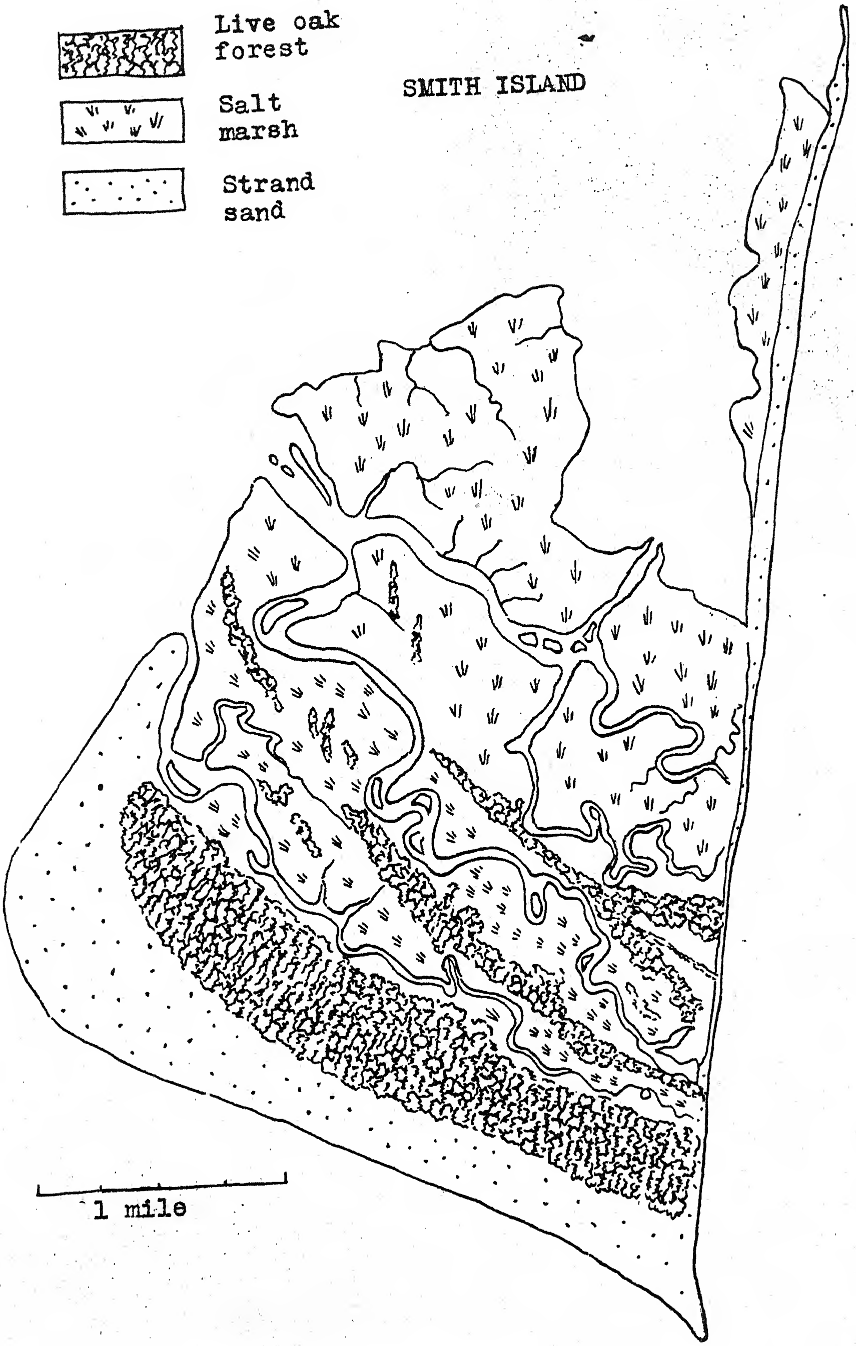

Fig. 1. Map of Smith Island showing distribution of live oak (*Quercus virginiana*) and other principal types of vegetation.

Thus, as a corollary of this discovery, it appears that on Smith Island which, because of its exposed position, is swept by spray during the higher winds, we observe the selection of the one dicotyledonous tree strongly resistant to this killing agent. A slow growing tree, yet requiring a favorable mesic, soil habitat, it may only attain dominance when freed from the competition of other trees, the hardwoods which cannot enter the spray zone. It is thus the spray factor which largely accounts for the statement that the live oak is a "tree of the sea coast."

In light of these observations a new and heretofore unrecognized type of climax becomes known. Such a climax may properly be called the "salt spray climax" which gives emphasis to the factor which brings the live oak to dominance.

Such a climax must have its seral story, which may be concisely given since the number of spray plants is highly restricted. The pioneer on the sand flats is, in the Cape Fear region, the sea oats (*Uniola paniculata*). This grass initiates the dunes and is the single dominant which can stand the high spray intensity. On older areas in the medium spray zone *Myrica cerifera*, *Ilex vomitoria* and often *Juniperus virginiana* come in as a shrub stage. This will be followed by the live-oak-forest climax.

The discovery of such a climax as the salt spray climax is of additional interest in connection with the concepts of mono-versus polyclimaxes. In this salt spray climax habitat we have a direct factor which is dependent upon an indirect climatic factor (wind) for its effectiveness. So long as the shore lines are relatively stable, this spray factor, which is even more stable, thus becomes a climax maker in its own peculiar way. This means that the usual coastal inland sere cannot take place on the ocean front and produce there the usual climax. It thus becomes necessary here to adopt the polyclimax concept for the general coastal region.

SUMMARY

Based upon observations reported recently (3), it has been found that live oak (*Quercus virginiana*) is the only broad leaved dicotyledonous tree, the mature leaves of which can withstand the destroying action of moderate salt spray.

Smith Island, a land area 3 miles wide at the Cape Fear angle of the eastern U. S. coast line, is covered with a nearly pure stand of very old climax live oaks, under which dogwoods indicate the high degree of soil maturity. Since we have shown that wind is not the factor controlling the zonation of the coastal dune plants and the form modification of the

woody ones, we are forced to the conclusion that in the history of the island, salt spray is the selective factor in bringing about the dominance and persistence of the salt-resistant live oak. It is further suggested that the spray factor largely accounts for the distinctive coastal distribution of live oak as a dominant throughout its range.

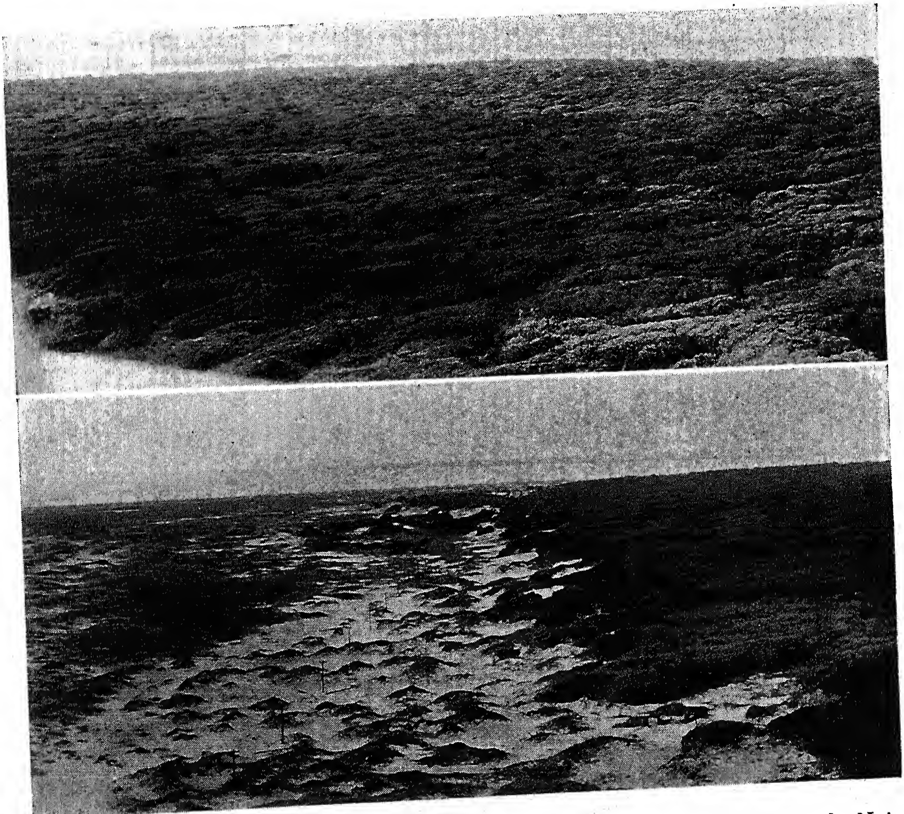

Fig. 2. Above. View across spray climax showing high dominance of live oak. Note striated appearance due to asymmetric growth of individual trees and tree groups. Below. Strand in front of forest on south side of the Island. Vertical lines are telephone posts. Both views taken from Coast Guard tower, 120 ft. high.

This discovery of a climax dependent upon a direct factor which in turn is dependent upon a climatic factor (wind) indicates that for the general coastal region the polyclimax concept must be held.

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